

Behavioural repertoire and the onset of precocious sexual behaviours in juvenile ruffs (*Calidris pugnax*)

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Abstract (227 words)

Adult phenotypes are shaped by developmental processes during early life. This also applies to reproduction and dominance-related behaviours before maturation, called precocious sexual behaviours. However, beyond largely anecdotal reports, the onset of such behaviours is rarely studied. Here we document the development of precocious sexual behaviours in the ruff *Calidris pugnax*, a lekking shorebird with pronounced sexual dimorphism and three genetically determined morphs that correspond to alternative reproductive tactics. To document how behaviours develop and diversify, we compiled a comprehensive ethogram in ruff chicks and examined age-related changes in behaviours. Using 6-min video recordings of interactions with a stuffed dummy chick, we analysed occurrence and duration of behaviours in 24 hand-raised chicks (3-15 days post-hatching, every other day). We documented 34 distinct behaviours belonging to five categories: ‘maintenance’, ‘movement’, ‘stationary’, ‘social non-sexual’, and ‘social precocious sexual behaviour’. Behavioural expression in chicks changed markedly with age, largely through shifts in the occurrence of a behaviour. Notably, ‘precocious sexual behaviours’ such as ‘circling’, ‘mounting’, and ‘strutting’, display and mating behaviours typical to adult ruffs, were already expressed from day 5 onwards, increasing in occurrence with age. This suggests that ruff chicks start to express motor coordination of these behaviours long before sexual maturity. The ethogram will function as framework for future analyses, for example to quantify sex, morph, and individual variation, and the developmental origins of complex social behaviours.

Keywords

behaviour, ontogeny, ruff, ethogram, precocious sexual behaviour, social behaviour.

34 Introduction

35 For most organisms, priorities in early life are growth and survival leaving other phenotypic traits
36 underdeveloped (Carrier and Leon 1990; Herrel and Gibb 2006). Only later do behavioural phenotypes
37 that are critical for adult life, such as social or reproductive behaviours, develop (Mason 1979; Veissier
38 et al. 1998). The timing of this transition is often unclear, particularly in the wild, where survival-
39 related behaviours can suppress other phenotypes. In birds, challenges during early development
40 include negotiating a trade-off between spending time on receiving parental care, such as being
41 brooded for thermoregulation to save energy, and spending time and energy on activity or social
42 interaction (Wekstein and Zolman 1971; Beintema and Visser 1989). A transition is also happening in
43 the antipredator defence behaviours, precocial chicks shift from being motionless and relying on their
44 cryptic plumage for camouflage (Colwell et al. 2007) to active avoidance through movement once their
45 mobility increases as they approach fledging age (Rohr-Bender et al. 2024). The necessary rapid
46 increase in mobility observed during the first two weeks of life is supported by sensory changes and
47 motor skill development. Ultimately, these developmental shifts enable the expression of novel
48 behaviours, such as more complex social interactions later in life (Bushnell and Boudreau 1993; Byers
49 and Walker 1995; Mellor and Lentle 2015), including behaviours that resemble those shown by adults
50 in the context of reproduction or dominance contests.

51 Precocious sexual behaviours are behaviours expressed by juveniles before reaching sexual maturity
52 that resemble those of adults shown during courtship or mating. These include early forms of
53 courtship, mating-like actions, or dominance-related displays (Andrew 1966; Schleidt 1970; Kramer
54 and Burghardt 1998; Kulik et al. 2015). Precocious sexual behaviours have been reported across a wide
55 range of taxa, including birds (Andrew 1966; Schleidt 1970; Schulman 1970), fish (Johnsson et al.
56 2001), reptiles (Kramer and Burghardt 1998), and mammals (Thwaites 1982; Young et al. 1982). For
57 instance, domestic chicks (*Gallus gallus domesticus*) perform copulatory movements within days of
58 hatching (Andrew 1966), showing that the motor patterns similar to adult sexual behaviour can
59 emerge very early in ontogeny. A related early-life phenomena that needs to be distinguished from
60 precocious sexual behaviours is sexual imprinting. The latter also occurs during early ontogeny and
61 shapes the preference for a future sexual partner typically without involving any precocious
62 expression of sexual behaviour (Lorenz 1935; Sluckin 2017). Yet, apart from some largely anecdotal
63 observations of precocious sexual behaviours, they remain relatively unexplored. In particular, little is
64 known about their developmental trajectory in species with reproductive diversity, such as
65 pronounced sexual dimorphism, clear sex roles or alternative reproductive tactics (Gross 1996;
66 Oliveira et al. 2008). Thus, investigating how and when precocious sexual behaviours emerge can
67 provide insight into ontogenetic emergence of adult sex roles including elaborate courtship
68 behaviours.

69 Establishing a qualitative baseline of the behavioural repertoire of a species is essential to investigate
70 further behavioural complexes, such as how sex and morph specific behaviours arise. Ethograms
71 provide such a framework by systematically defining and categorising behaviours (Huxley 1914; Lorenz
72 1935; Schleidt et al. 1984). Since their early development, ethograms have been central tools in
73 behavioural research, supporting reproducibility, inter-study comparability (Schleidt et al. 1984; van
74 Sluys et al. 2024), and applications in conservation, captive breeding, welfare assessment, and
75 evolutionary ecology (Sutherland 1998; Barman and Sharma 2017; Greggor et al. 2019; Gräfe and

Stuhrmann 2022; van Sluys et al. 2024). Ethograms typically cover broad behavioural domains such as maintenance, movement, social, reproductive, and anti-predator behaviours. While ethograms are well established for many species in adults, detailed descriptions, complete for all behaviours during early life are far less common. Precocial birds are particularly valuable in this context. Since they are mobile and largely self-sufficient from hatching, precocial chicks can already express a broad behavioural repertoire including social behaviours early in life (Scheiber et al. 2017). This allows researchers to track the emergence of behaviours that may foreshadow adult phenotypes, including social roles, hierarchies, and reproductive strategies.

We studied the onset of precocious sexual behaviours in young ruffs (*Calidris pugnax*). The ruff is a lekking shorebird with striking sexual dimorphism and an complex mating system (Hogan-Warburg 1966; van Rhijn 1991; Lank et al. 1995; Widemo 1998; Jukema and Piersma 2006; Lank et al. 2013), making it an ideal species for studying the ontogeny of sex- and morph-specific behaviours. Adult males are approximately 70% heavier than females (Münster 1990; Meissner and Zięcik 2005; Lank et al. 2013; Giraldo-Deck et al. 2020) and exhibit three genetically determined morphs that are present in both sexes: Independents, Satellites and Faeders (Küpper et al. 2016; Lamichhaney S et al. 2016). In males, these morphs correspond to alternative reproductive tactics. “Independents” that defend territories aggressively, non-aggressive “Satellites” that form coalitions with Independents, and rare “Faeders” who mimic females and employ sneaky mating tactics (Jukema and Piersma 2006; Lank et al. 2013). Within both sexes, Independents are the largest, Satellites intermediate, and Faeders the smallest in size (Lank et al. 2013; Giraldo-Deck et al. 2020). In females, the morphs impact reproductive success and physiology (Giraldo-Deck et al. 2022; Loveland et al. 2022). However, no consistent morph-specific behavioural differences have been reported. Much less is known about early ontogeny in this species. At hatching, males and females are similar in size, but sex differences become visible within the first week of life, and morph differences in growth rate emerge around the second week (Giraldo-Deck et al. 2020). Like other waders, ruff chicks are precocial, gaining mobility almost immediately after hatching and making independent behavioural decisions early in life (Colwell et al. 2007). Already during the first two weeks, rapid sensory and motor maturation leads to the emergence of sex and individual differences in activity (Rohr-Bender et al. 2024) suggesting that behaviour differences between the sexes may arise early in life, to a lesser extent, the same might be the case for morph differences. Studying this developmental phase thus provides a crucial window into how early behaviour may underpin later adult reproductive strategies.

To investigate the emergence of early social and precocious sexual behaviours, we designed an experiment using a stuffed dummy chick to simulate a smaller, submissive conspecific. This approach has previously been shown to elicit behaviours in early ontogeny that are otherwise rare or inhibited in live–live interactions (Schein and Hale 1959), because siblings may actively resist or not tolerate them (personal observation). The dummy thus provided a controlled context to observe a broader range of behavioural responses that might otherwise remain hidden or occur too infrequently to be able to study systematically. Using this setup, we first established a detailed ethogram of young ruffs during the first two weeks of life and second, explored the developmental trajectories of individual behaviours. Specifically, we asked (i) in how many individuals does a behaviour occur, (ii) how long does the behaviour last, and (iii) how does the occurrence and duration of a behaviour change with age.

Methods

Study population

We investigated chicks (3–9 days old) and juveniles (11–15 days old) from a captive population of ruffs housed at the Max Planck Institute for Biological Intelligence, Seewiesen, Germany, during the 2022 breeding season. The population was established from eggs collected near Oulu, Finland, in 1985, 1989, and 1990, which were hatched and maintained at Simon Fraser University, Canada, before being transferred to Seewiesen in 2019. Additional individuals originating from the Netherlands, Belgium, and Germany were later incorporated (Lank et al. 2013; Rohr-Bender et al. 2024). Eggs were artificially incubated, chicks were hand-raised, individually marked with colour rings, and sex and morph were determined using diagnostic SNP markers (Giraldo-Deck et al. 2020). Rohr-Bender et al. (2024) provided an in depth description of the rearing procedures used. During the first 9–10 days, chicks were housed in groups of up to eight in plastic boxes (Housing type ‘box’: 60 × 40 × 32 cm) with soft lining and a shelter. On day 10, a day when no trials were planned, they were transferred to indoor aviaries (Housing type ‘room’: 2 × 3 m) holding up to 26 juveniles. Around day 33, juveniles were integrated into the adult flock, which is housed in a large aviary of approximately 300 m². Throughout development, birds were kept in mixed-sex and mixed-morph groups of similar age with *ad libitum* access to food and water.

Experimental setup

The purpose of the experimental setup was to enable us to investigate behavioural interactions of chicks with each other and with a dummy chick. The dummies were chicks from our own population that died during earlier years and were stuffed by a taxidermist. They simulated a slightly smaller, submissive conspecific to elicit behaviours that are typically rare or inhibited in live-live chick interactions and might not be tolerated among siblings.

We used six dummies dependent on the focal chicks’ average size: two small (60 mm × 20–25 mm) until ~day 4, two medium (70 mm × 25 mm) from day 5–9, and two large dummies (90–110 × 50–60 mm) from day 10–15. All dummies exhibited a submissive natural crouching posture.

We recorded each trial for at least six minutes. In the ‘box’ trials, we mounted a camera (Nikon Coolpix B700 or Canon EOS 750D with EFS 18-55mm objective) on a tripod and filmed from slightly above the box wall. In the ‘room’ trials, a wall-mounted surveillance camera (Axis M2026-LE Mk2 4K) recorded the juveniles from a side view. All cameras recorded with 25 frames per second. Chicks interacted freely with the dummy and with each other without human disturbance. We conducted most trials (90%) in the morning between 08:00 and 13:00, with a few extending into the afternoon (no later than 17:15).

We conducted the experiment daily with all 115 hand-raised individuals. Because of time constraints we restricted the analysis to a random subset of 24 individuals, balanced across sex and morph (four per combination) with detailed manual behavioural coding data. Each selected chick was analysed at ages 3, 5, 7, and 9 days (box trials) and 11, 13, and 15 days (room trials).

Ethogram construction and behaviour coding

We developed a comprehensive ethogram of behaviours shown by ruff chicks through a combination of literature research and a preliminary coding trial. We first surveyed published ethograms of birds,

including both adult and juvenile stages, to ensure that all major behavioural categories, which are ‘maintenance’, ‘movement’, ‘stationary’, ‘social non-sexual’, and ‘social precocious sexual behaviour’, were represented (Andrew 1966; Schleidt 1970; Schulman 1970; Vidal 1971; Schleidt et al. 1984; Barman and Sharma 2017; Simian et al. 2024; van Sluys et al. 2024). Next, we coded the first three minutes of day-9 box trials (or day-7 if day-9 was unavailable) for all individuals in the selected subset. During this phase, we added behaviours as they occurred and refined definitions until the ethogram was consistent and comprehensive. Afterwards, we rechecked all preliminary observations against the final definitions. In the subsequent main coding phase, we added five behaviours (14.7 %) that did not occur previously and made minor adjustments to the behavioural definitions.

The start of the observation period varied with housing type. For chicks in boxes, the trials started immediately after the dummy had been placed in the centre and the experimenter’s hand was out of frame. For juveniles in indoor aviaries, the experimenter first carefully herded the juveniles into the front half of the aviary, which is separable from the second half of the room, closed it off, and placed the dummy on the ground in front of the camera towards the middle of the room before leaving. Because this procedure caused a greater disturbance than in the box trials, we began the behavioural coding one minute after the experimenter had left the room to give the juveniles some time to adjust. All observation periods lasted six minutes, regardless of the housing type.

We coded all videos in BORIS (version 8.27.1; Friard and Gamba 2016). For each focal individual, we coded every behavioural bout it performed as a state event by documenting the start and end time. ‘Defecation’, ‘Aggressive pecking’, and ‘Silent cackle’ we coded as point events and later translated into state events with a fixed length of one frame (0.04 s). We coded most behaviours frame-by-frame. Only ‘Walking’ and ‘Alertness’, we coded second-by-second because their high frequency made frame-by-frame coding too time consuming. The coding of all videos was split between three coders. All were blind to the sex, morph, and identity of the focal chick to avoid bias (Burghardt et al. 2012).

As a quality control, we assessed inter-coder reliability for a random subset of eight observations using intraclass correlation coefficients (ICC). Agreement between coders was very high across the dataset (overall ICC = 0.97, 95% CI: 0.96–0.98, Supplement “Coder reliability analysis”).

Data processing

We exported the raw data from BORIS and processed all subsequent steps and statistical analyses in R (version 4.4.1; R Core Team 2024). To ensure consistency, we applied a matrix of rules specifying which behaviours could or could not occur simultaneously (Table S2). For each observation, we then calculated time budgets as the total duration of each behaviour of the focal individual. These totals were corrected for periods when the focal chick was partly or fully hidden from the camera (Table 1).

Statistical analysis

Because housing conditions differed substantially between boxes and rooms, we analysed each period separately. However, since all chicks transitioned to the new housing type at the same age, the effects of age and housing type could not be disentangled. For each behaviour–housing type combination, we fitted a Gamma Hurdle Model (GHM) with a log link function using the *brms* package (version 2.22.0; Bürkner 2017). GHMs are well suited to handle response variables with zero-inflation such as many behavioural variables. The models operate with two parts, the hurdle and the conditional part. The hurdle part models the predicted probability of a certain behaviour occurring at each age

(‘occurrence’) as a binary process (‘0’, ‘1’), while the conditional part models the duration of a certain behaviour when it occurs (‘mean duration’) using a Gamma error distribution.

To ensure comparability across behaviours and to account for limited sample size, we applied the same basic model structure for all models. The cube-root transformed ‘total duration of the behaviour’ was used as the response variable with ‘age’ (day 3, 5, 7, 9 for box trials; day 11, 13, 15 for room trials) fitted as fixed effect, and ‘individual ID’ (24 levels) as random intercept. This fixed and random effect structure was used for both the hurdle and conditional parts of the model. For model fitting, we adjusted ‘adapt delta’ to the lowest value that avoided divergent iterations with an upper limit of 0.99. If divergent iterations nevertheless occurred, results were not further interpreted (Supplement, “Results Tables”). For behaviour–housing type combinations with fewer than three non-zero observations, we did not run statistical models.

Results

Of the 168 planned trials, 160 were successfully conducted. Eight trials were missing due to technical or identification issues (Supplement, “Experimental trial completion”). The trials were recorded across 103 videos, meaning that some observations of different chicks originated from the same video recording.

Ethogram

We observed 34 distinct behaviours, which we grouped into five categories: ‘maintenance’, ‘movement’, ‘stationary behaviour’, ‘social, non-sexual behaviour’, and ‘social, precocious sexual behaviour’ (Table 1). Example images and clips are provided in the supplement (Figure S2-S6, Table S1). Some behaviours were specific to one housing type. For example, ‘walking’ and ‘alertness’ were only coded during the box trials, even though these behaviours also occurred in the room phase. Both behaviours were coded second-by-second, because a frame-by-frame approach used for all other behaviours would have been too time-consuming given how frequently they occurred. However, this second-by-second focal coding was not feasible in the larger and more crowded room environment, where increased movement and frequent overlap among individuals made it difficult to reliably follow the focal chick. Conversely, ‘in water bath’ and ‘bathing’ were only observed in the room trials, as water baths were not available in the boxes. We distinguished between ‘sitting near dummy’ and ‘sitting elsewhere’ to capture potential social interactions with the dummy. ‘Sitting near dummy’ often occurred during a visitation or other interaction with the dummy and separating it from ‘sitting elsewhere’ allowed us to isolate these specific social interactions from general sitting behaviour. We did not include ‘standing’ as a separate behaviour, as it essentially represents the residual time when chicks were neither walking, sitting, nor crouching, and can therefore be inferred from these categories without adding new information.

(Table1)

Changes in occurrence and duration of the different behaviours with age

Across all behavioural categories, behaviours could be broadly divided into two groups: frequent and rare behaviours. Frequent behaviours were expressed by more than half of the individuals in at least one trial, and rare behaviours were shown by fewer individuals (, A – Overall, Table S1). Visually comparing the raw data indicated that housing type affected the occurrence but not the duration of several behaviours. However, since analysed the housing types in separate models, comparability across the full age range of the 24 individuals tested is limited. In particular, behaviours classified as

‘stationary behaviour’, ‘social, non-sexual’, and ‘social, precocious sexual’ occurred more often in box than in room trials (, A). Clear age-related changes in behaviour were also more evident in the box trials than in the room trials (). Regardless of the of housing type, age-related changes in the ‘occurrence’ of behaviours were more frequent (10 behaviour–housing type combinations increasing, 4 decreasing with age) than changes in the ‘mean duration’ (3 increasing, 3 decreasing;). For 15 behaviour–housing type combinations, mostly in room trials, no models could be fitted because the behaviour occurred less than three times. A further 10 models converged only with divergent iteration warnings, rendering their results less reliable. These cases were excluded from interpretation (; Table S3-S10).

In the ‘maintenance’ category, the occurrence of behaviours clearly changed with age for ‘foraging’, ‘head scratching’, ‘shaking body parts’, and ‘head shaking’ in the box trials, and for ‘in water bath’ in the room trials (, A). Only ‘defecation’ in room trials showed a clear change in mean duration (, B; Table S3-S5).

In the ‘movement’ category, clear age effects on occurrence were detected for ‘walking’, ‘jumping’, ‘stereotypic behaviour’, ‘head scratching’, and ‘uncoordinated behaviour’ (box trials), and for ‘uncoordinated behaviour’ in room trials, the latter with a model warning about divergent iterations (, A). A clear age effect on mean duration was found only for ‘uncoordinated behaviour’ in the box trials (, B; Table S6-S7).

‘Stationary behaviours’ occurred exclusively in box trials. Only ‘staying frozen’ showed an age-related change in occurrence, though with a divergent iteration warning (, A). In contrast, ‘sitting elsewhere’ in room trials was the only behaviour in this category to show an age-related change in mean duration (, B; Table S8).

In the ‘social, non-sexual behaviour’ category, we detected no clear age-related changes in occurrence (, A). However, mean duration changed with age for ‘visitation’ and ‘pecking or touching’ in the box trials (, B; Table S9).

‘Social, precocious sexual behaviours’ were mainly expressed during box trials and only rarely by older juveniles in the room trials. We detected clear age-related changes in occurrence but not mean duration for ‘circling’, ‘mounting attempt’, and ‘mounting’ (). Finally, ‘strutting’ and ‘silent cackle’ were among the rarest behaviours across all categories, being shown by only 25% and 16.7% of individuals overall and occurring only in six and four trials, respectively (, A; Table S10).

(Figure 1)

Discussion

Understanding behavioural variation during early ontogeny is critical for interpreting the developmental trajectories that shape adult phenotypes. However, in comparison with adults, behavioural variation in juveniles is much less characterised in most taxa. Here, we provide a comprehensive ethogram of young ruffs, covering both non-social and social behaviours. By systematically documenting the full behavioural repertoire of 24 individuals observed during short behavioural trials to elicit social behaviours during the first two weeks of life, we offer a baseline for exploring age-dependent, sex-specific, morph-specific, and individual variation. This systematic

characterization of different behaviours allows us to assess how rarely expressed behaviours, such as precocious sexual behaviours, emerge and change over time, and may stimulate further studies that explore how functional and developmental mechanisms may shape the early expression of different behaviours. Our study thus combines a broad descriptive framework with quantitative examination of the occurrence and duration of behaviours during the early ontogeny in a highly polymorphic species.

Ethogram

We provide a detailed ethogram for the chicks in a precocial bird species with high behavioural variation. We focus on a very early developmental phase, a part of the developmental process that has received comparatively little attention so far. We specifically included precocious sexual behaviour, for which some studies have addressed similar age periods. However most avian research has concentrated on poultry (Andrew 1966; Schleidt 1970; Vidal 1971), and detailed work on non-model species such as ruffs remains scarce. In these poultry studies, juvenile sexual displays typically include 'mounting' and 'strutting', which are also present in ruffs. However, 'circling' appears to be specific to ruffs and has not been reported in the early ethograms of other species. This comprehensive ethogram offers a solid foundation for future studies, for example, to investigate sex- and morph-specific differences in the expression of different social behaviours.

Changes in occurrence and duration of the different behaviours with age

We found that the onset and expression of different behaviours varied strongly with age, indicating that age is a major determinant of behavioural development in young ruffs. Our statistical approach using GHMs allowed us to separate two key aspects of behavioural development: changes in the 'occurrence' and 'mean duration' of behaviours. Some behaviours were expressed only infrequently or by a few individuals, which could reflect true individual variation or limitations of the study design and/or housing. For example, short-duration behaviours are easier to miss during coding than longer ones. Increasing sample size or trial duration would improve detection, but the time-intensive nature of manual coding imposes a trade-off: examining longer or more videos means that fewer individuals or fewer days can be analysed. We also observed that the housing environment influenced behavioural expression. Age-related changes were stronger during the box than the room trials. This might reflect that morphological and physiological development is particularly rapid immediately after hatching and slows with age (Ricklefs 1979), which likely also enables the chicks' behavioural repertoire to develop faster during that period. After juveniles transitioned to the larger rooms, we observed that behaviours directed towards the dummy were performed by fewer individuals. This reduction may reflect the more complex environment, with higher overall activity, perhaps greater agitation, and more conspecifics available for interactions. This likely made the dummy less conspicuous or attractive. However, we cannot exclude an age-related change in behavioural motivation or expression. Nevertheless, when behaviours were expressed, their mean duration was comparable to the mean duration observed in the box trials, suggesting that the behaviours were dormant and the housing context elicited specific behaviours at different frequencies among juveniles.

Behaviours in the categories of 'maintenance', 'movement', and 'stationary behaviour' reflected the interplay of changing motor skills, physiological demands, and environmental context. As chicks grew, they likely needed to meet basic needs such as feeding and drinking less frequently, as they could ingest larger amounts of food per bout (Kitaysky 1999; Dwyer et al. 2002). At the same time, they likely became more efficient in handling food and water, making behaviours like 'head shaking', often

used to expel excess food or water, less necessary. Locomotor activity was consistently present throughout development, but we observed that balance and coordination, initially likely a challenge given their long legs, seemed to improve with age. Consequently, 'uncoordinated behaviour' decreased, while more demanding movements such as 'jumping' emerged. Older chicks also appeared to require shorter breaks from strenuous activity, reducing the likelihood of observing extended 'stationary behaviour' periods within the short test duration. Furthermore, individual motivation and personality likely influenced all aspects of behavioural development, shaping both the timing and frequency of expression (Hertel et al. 2023). For example, 'in water bath' likely reflected a combination of individual discovery and social learning, as juveniles encountered this novel feature in the larger room. Predator-evasion behaviour occurred only rarely, likely reflecting the familiar, low-threat conditions of the housing environment. In this context, 'staying frozen', a typical response to a potential threat, can be considered a precursor to the crouching reflex, where chicks flatten their bodies to the ground and rely on cryptic plumage to avoid detection (Simmons 1955; Colwell 2010; Volkmer et al. 2024). Finally, we observed 'stereotypic walking behaviour' in a small but increasing number of chicks with age. Such behaviour is often interpreted as a stress response to limited space (Mason et al. 2007) and may have reflected the restricted size of the boxes, which became proportionally smaller as chicks grew.

Our category 'social, non-sexual behaviour' contained social behaviours that were consistently expressed at different frequencies. 'Alertness' was shown by nearly all chicks, at consistently high levels across all analysed ages. This suggests it is an inherent requirement for survival under a constant predation threat from an early age until fledging (Colwell et al. 2007), though the broad coding definition may also have contributed to its frequent detection. 'Visitation' and 'pecking or touching' were also frequently observed, and their duration increased with age during the box phase. This pattern may indicate that older chicks have more energy available for social interactions once basic needs are met, while younger chicks face stronger trade-offs with feeding, drinking, or thermoregulation (Burghardt 1988; Schekkerman et al. 2001). The behaviours may also reflect the development of social and cognitive skills, such as curiosity and exploration. However, since we do not know whether the chicks recognized the dummy as a conspecific, the behaviours could also represent responses to a novel object rather than social interaction per se. In contrast, 'aggressive pecking' and 'avoidance' were only rarely observed across ages. This rarity likely reflects the generally non-antagonistic nature of the species, outside the high-conflict periods of adult male courtship during the breeding season. Aggressive interactions over food are uncommon in both juveniles and adults, even when experimentally provoked (L. Giraldo-Deck and K. Kupán, personal observation). 'Avoidance' may also be shown through very subtle social cues that might not be detectable by human observers, suggesting the true frequency could be higher than recorded.

Our experiment successfully triggered precocious sexual behaviours in response to the submissive dummy chick, although they remained uncommon in comparison with other behaviours. 'Circling', 'mounting attempts', and 'mounting' were mostly observed during the box trials and less frequently afterwards. The increase in the number of chicks showing these behaviours with age suggests that they may require higher physical and social skills, relying on either a learning process, or the motivation to show the behaviours only develops with time. Precocious sexual behaviours are often interpreted as precursors of adult mating, as the behavioural patterns resemble those seen in adults. Ruff chicks in this study already performed such behaviours at 5 days of age, similar to the earliest

observations in poultry (Andrew 1966; Schleidt 1970; Schulman 1970; Vidal 1971), highlighting that such behaviours can emerge very early in development. In ruff chicks, this occurs much earlier than previously assumed, as earlier behavioural observations reported that captive chicks did not engage in clear social interactions before day 6 post-hatching, and that ritualised adult-like behaviours such as bill thrusting, forward display, or first copulation attempts were only observed around 30 days of age (van Rhijn 1991). Several functional explanations may account for the early occurrence of these behaviours. The precocious sexual behaviours could represent a form of social play, in which elements of adult behaviour are rehearsed in a low-cost context (Burghardt 2005; Pellis S and Pellis V 2013). Alternatively, they might help establish dominance relationships among peers (Queiroz and Cromberg 2006) or function as behavioural rehearsal for adult mating, potentially enhancing later reproductive success (Mason 1965; Byers and Walker 1995). At the same time, also developmental mechanisms may influence the expression of precocious sexual behaviours. Increasing motor skills may enable chicks to perform the complex movements involved (Byers and Walker 1995), while hormonal changes with age could further shape motivation. Experimental evidence supports this link, as testosterone injections were found to increase precocious sexual behaviours in turkeys and chickens (Schein and Hale 1959; Andrew 1966; Schleidt 1970). In ruffs, androgens such as testosterone and androstenedione that may elicit precocious sexual behaviours have been detected in the blood of ruff chicks (Giraldo-Deck et al. 2024). Moreover, androgen levels fluctuate strongly during early ontogeny in ruffs suggesting that endocrine changes may also contribute to the timing and frequency of expression. Thus, both functional and developmental mechanisms probably contribute jointly to the early expression of precocious sexual behaviours in ruff chicks.

Conclusion

We provide a qualitative ethogram that documents a broad behavioural repertoire in ruff chicks. We show quantitatively that age-related changes in both social and non-social behaviours are reflected more often in the occurrence rather than in the mean duration of behaviours. Housing context shaped behavioural expression, with clearer ontogenetic patterns in the box than in the room trials, underscoring the role of social and environmental conditions in eliciting many behaviours.

Importantly, we documented the expression of precocious sexual behaviours from an age of five days onwards. They increased in occurrence until the age of nine days, while mean duration showed little variation. Precocious sexual behaviours were expressed towards the dummy chick primarily in the box context, suggesting that developmental readiness and immediate social context govern their expression. They were rare among older juveniles during room trials although the change of the social settings from box to room housing complicates the interpretation of age-related patterns across the full observation period. Together, these results provide a baseline for more quantitative work on the ontogeny of social and non-social behaviours. Future studies should address whether precocious sexual behaviours vary between sexes and morphs, ideally in larger sample sizes.

Author Contributions

Veronika A. Rohr-Bender: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, interpretation of results, visualization, writing – original draft, writing –

review and editing. Udit Nair: data curation, formal analysis, investigation, methodology, interpretation of results, writing – review and editing. Lina M. Giraldo-Deck: conceptualization, methodology, interpretation of results, writing – review and editing. Krisztina Kupán: formal analysis, methodology, writing – review and editing. Rebecca Pederson: investigation, methodology, writing – review and editing. Clemens Küpper: conceptualization, formal analysis, funding acquisition, methodology, interpretation of results, resources, supervision, writing – original draft, writing – review and editing.

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Ethics statement

All procedures involving animals fully adhered to the European Directives for the protection of animals used for scientific purposes (2010/63/EU)]. Animal breeding and housing was conducted under permit 341.5-5682.1/1-2021-003 by Landratsamt Starnberg. No animals were harmed during the experiments.

Conflicts of interest

The authors declare no conflicts of interest.

Data availability

Example video clips, all data tables containing the raw behavioural codings, a table containing the birds' information, and scripts are stored on Edmond (<https://doi.org/10.17617/3.7PIHZQ>).

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601 Tables

602 “Table 1.” Complete ethogram of all behaviours observed in ruff chicks during early development (age: 3 days
603 to 15 days). The “target” is either the dummy or a sibling. The total duration of all behaviours was corrected for
604 periods when the focal chick was completely hidden from the camera.

Category	Behaviour	Description
Maintenance	Foraging ^a	The subject pecks on an item other than the dummy or siblings, such as food in the bowl or objects on the ground.
	Carrying object ^a	The subject picks up an item, such as food, and moves forward with it holding the item in the bill.
	Drinking ^a	The subject dips its bill into water and often follows by lifting the head and performing swallowing movements.
	Defecation ^b	The subject discharges faeces.
	In water bath ^c	The subject steps into the water bath and stands or moves around in it. Other behaviours such as ‘drinking’ or ‘bathing’ can occur simultaneously.
	Bathing ^c	The subject submerges and splashes in the water bath.
	Preening	The subject organises and cleans its own feathers with the bill on the belly, neck, back, or wing areas.
	Head scratching	The subject uses one foot to scratch its head.
	Self-pecking (ring/leg)	The subject pecks with its bill on its own ID rings or leg.
	Shaking body parts	The subject rapidly shakes parts of its body, such as the wings or body feathers (rousing), or their legs.
	Head shaking ^a	The subject shakes its head side to side, sometimes very shortly.
	Stretching extremities	The subject extends one or more limbs away from the body for up to a few seconds in a slow movement.
Movement	Yawning ^a	The subject gapes its bill open in a slow movement, remains open briefly (up to 1 s), then closes the bill rapidly and does not repeat immediately.
	Walking ^d	The subject steps forward at any pace. Other movement-related behaviours are coded in parallel.
	Running	The subject moves forward faster than normal and even speed.
	Jumping	The subject pushes off the ground into the air with both legs, typically for an out of reach object.
	Flapping wings	The subject moves its wings up and down, sometimes additionally making small hops.
	Stereotypic behaviour	The subject walks back and forth repetitively and aimlessly next to a wall.
Stationary behaviour (other behaviours can occur simultaneously)	Uncoordinated behaviour	The subject slips, falls, or shows clumsy movements.
	Sitting near dummy	The subject sits on its tarsi close to the dummy (maximum distance: body length of the chick) without the belly touching the ground.
	Sitting elsewhere	The subject sits down on its tarsus without the belly touching the ground, either near a sibling or alone.
	Crouching	The subject lies completely flat on the ground with the belly in contact with the surface.

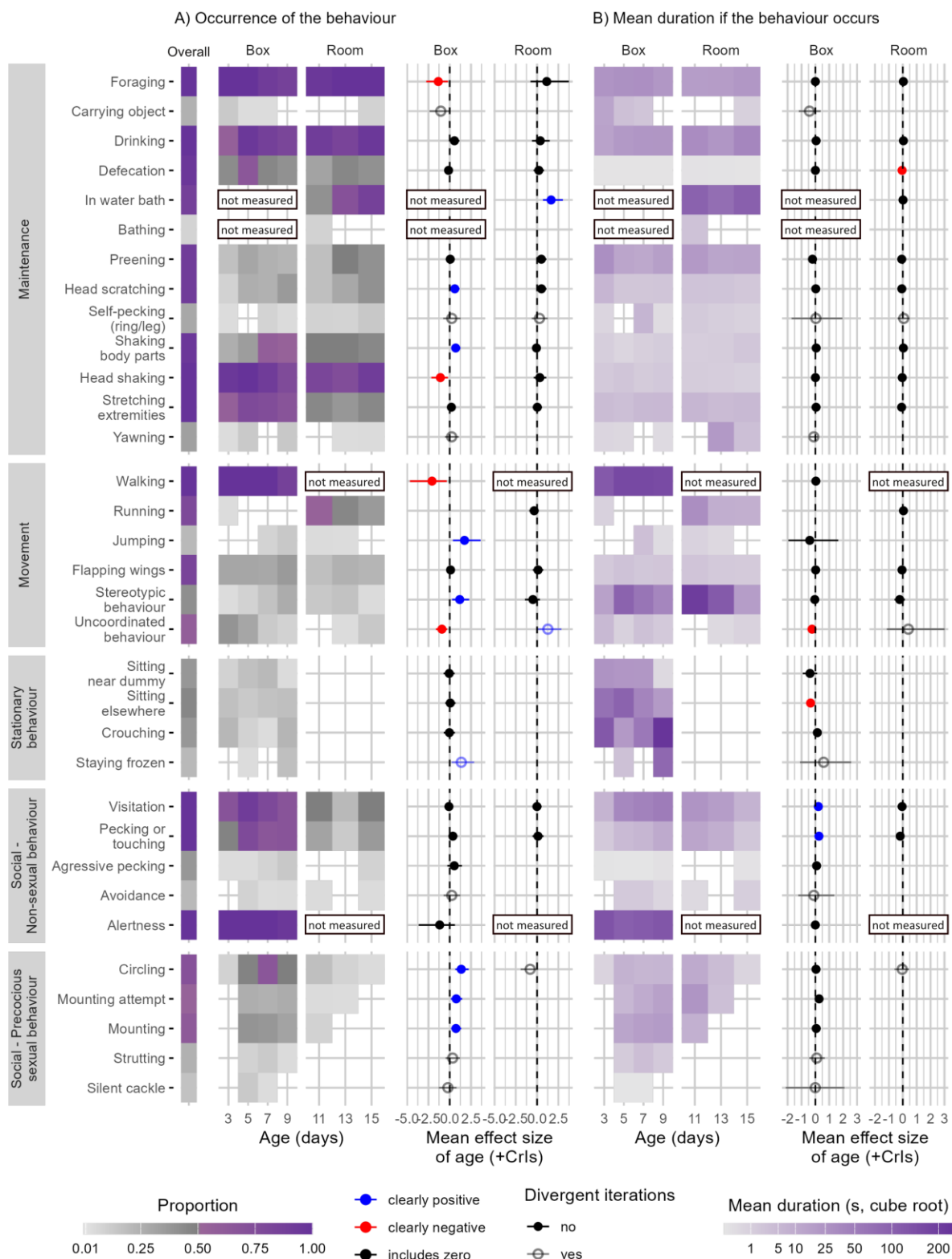
	Staying frozen	The subject remains completely motionless for an extended period, in any posture. No other behaviour can occur simultaneously.
Social, non-sexual behaviour	Visitation	The subject approaches a target with eyes and bill directed towards it. Other social behaviours might occur simultaneously. If the subject's gaze shifts away, visitation is interrupted until focus resumes. Visitation lasts until the subject leaves the target.
	Pecking or touching ^a	The subject makes physical contact with the target using the bill, either fast and shortly (pecking) or slowly and gently (touching). Pecks or touches occurring during precocious sexual behaviours, like 'mounting', 'mounting attempts', or 'circling' are excluded.
	Aggressive pecking ^{a, b}	The subject delivers pecking movements to the target like in 'pecking or touching' but in a forceful way. This is a subcategory of 'pecking or touching' and recorded in addition to it.
	Avoidance	The subject withdraws or moves away in response to a sibling's approach, such as 'aggressive pecking', 'mounting', or 'strutting'.
	Alertness ^{a, d}	The subject scans its surroundings, while raising its head and looking around, straight outwards or upwards.
Social, precocious sexual behaviour	Circling	The subject walks around the target with sideways steps, holding the bill pointed towards the target.
	Mounting attempt	The subject stands on the target or over it without fully bending the legs, often pecking at the target's head. The bill is usually directed downwards.
	Mounting	The subject climbs onto the target and sits on it. Sometimes accompanied by tail shaking or pecking the target's head. The bill is typically held downwards.
	Strutting	The subject presents itself in front of the target with a horizontal or slightly raised posture, sometimes pacing, bill often held down or moving up and down, and occasionally neck feathers are fluffed.
	Silent cackle ^{a, b}	The subject makes nodding head movements with the bill half open, usually while standing upright. This usually occurs during a 'mounting attempt' or 'strutting'.

^a The total duration of the behaviour was additionally corrected for periods when the focal chick's head was not visible.

^b Coded as point events with the standard length of 0.04 s.

^c Water baths were present only when juveniles were housed in larger rooms.

^d Coded second by second, only while chicks were housed in the boxes.



612

613 **Figure 1**

Figure Captions

Fig. 1. Quantitative ethogram showing the occurrence and duration of behaviours in ruff chicks during early ontogeny (age 3–15 days). Chicks experienced two housing conditions that required separate analysis due to limited comparability: first in small groups (2–8 chicks) in a small ‘box’ without access to a water bath, where ‘in a water bath’ and ‘bathing’ did not occur; and later in a larger ‘room’ with larger groups (up to 26 chicks), where ‘walking’ and ‘alertness’ could not be quantified reliably due to the crowding. Consequently, separate Gamma Hurdle models (GHM) were run for each combination of behaviour and housing type. (A) Occurrence: raster plots show the proportion of chicks performing each behaviour, with colours shifting from grey to purple when more than half of the group displayed the behaviour. The first raster plot column shows the overall proportion of chicks showing the behaviour at least once during any of the trials. Effect size plots show the mean age effect ($\pm 95\%$ credible intervals (Cris) from the hurdle part of each GHM. (B) Mean duration: raster plots show raw group means if behaviours occurred. Effect size plots show the mean age effect ($\pm 95\%$ CrIs) from the conditional part of each GHM. In both effect size plots, closed versus open circles indicate whether divergent iterations occurred even at an ‘adapt delta’ of 0.99, in which case we did not interpret the results further. No effect size was plotted if fewer than three non-zero observations occurred in the subset of data.

Behavioural repertoire and the onset of precocious sexual behaviours in juvenile ruffs (*Calidris pugnax*)

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Supplementary Material

Experimental trial completion – Overview

We conducted four planned trials on days 3, 5, 7, and 9 of age in the box phase, and three additional trials on day 11, 13, and 15 in the room phase. Not all trials could be analysed as planned (Figure S1). In total, 168 trials were planned for 24 individuals, of which 95.2 % were conducted as intended. A small proportion of trials (4 trials, 2.4 %) were shortened due to technical issues (e.g., battery failure, full memory card) or observational problems (individual identification impossible during room trials). Further trials were missing because the recording failed entirely (8 trials, 4.8 %).

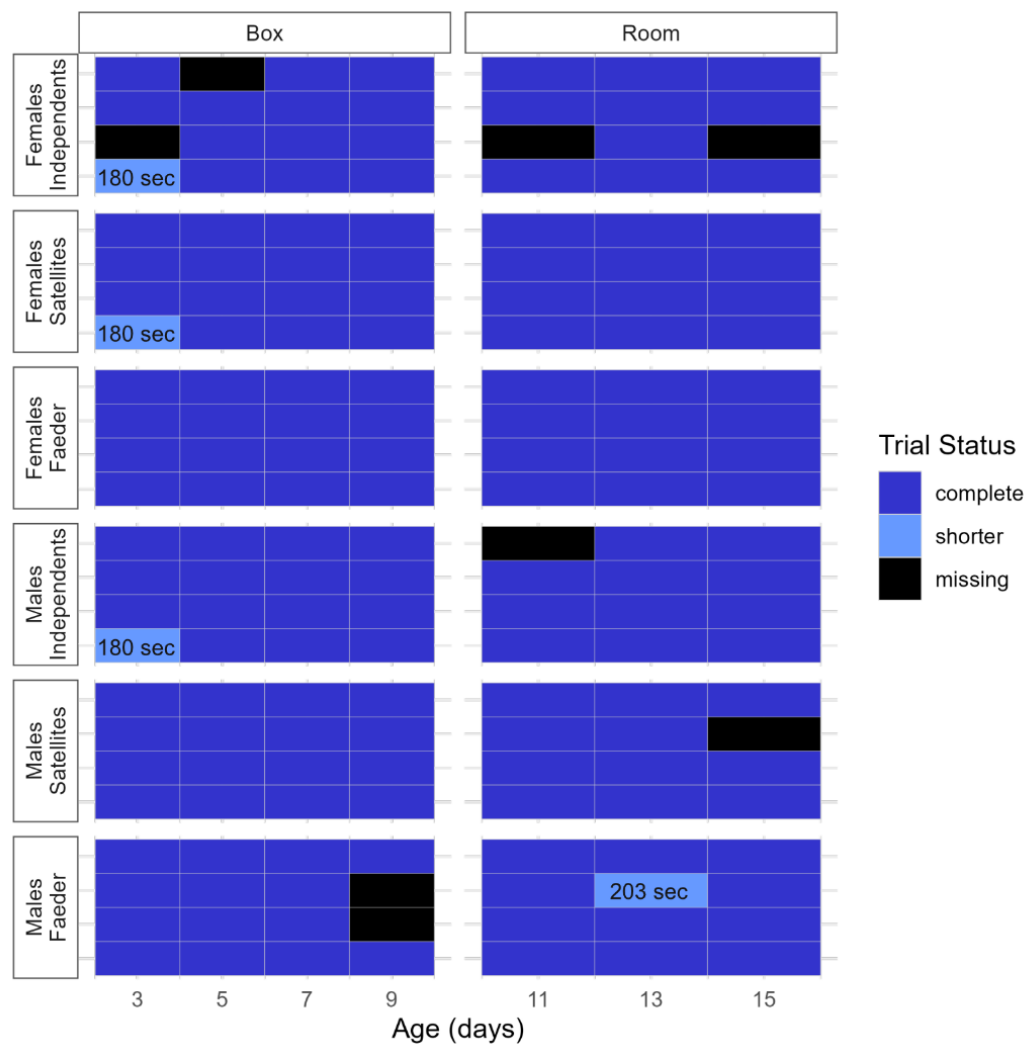
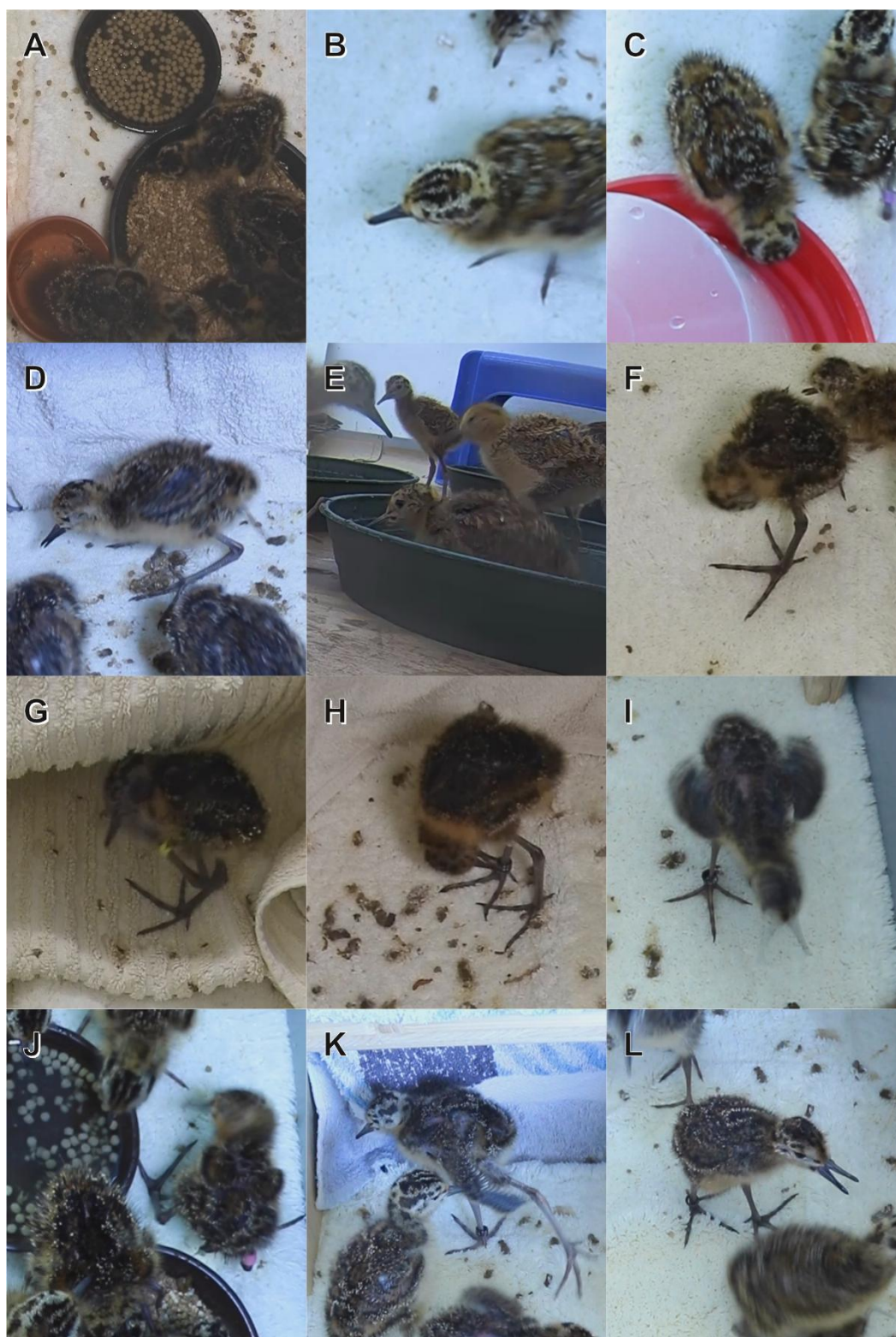


Figure S1: Overview of experimental trial completion for ruff chicks during early ontogeny under two housing conditions. Each row represents one individual chick, with columns showing the planned behavioural trials at different ages (days 3, 5, 7, 9 while being housed in a box; days 11, 13, and 15 while being housed in a larger room). Panels are split by sex-morph groups (female Independents, Satellites and Faeder, and male Independents, Satellites, and Faeder). Trial status is indicated by colour: dark blue = completed trial (full 6-minute observation period), light blue = shorter trial (recording interrupted due to technical issues such as battery failure or reliable identification was not possible any longer), black = missing trial (video recording or behavioural coding failed entirely).

Ethogram – Images & Example clips

The ethogram comprised 34 distinct behaviours, which we grouped into five categories: 'Maintenance', 'Movement', 'Stationary behaviour', 'Social, non-sexual behaviour', and 'Social, precocious sexual behaviour' (Table 1). To illustrate the behavioural definitions, we provide example images for each category (Figure S2-Figure S6). In addition, example video clips of all behaviours (Table 1) are stored on Edmond (<https://doi.org/10.17617/3.7PIHZQ>). These materials are intended to clarify the coding criteria and provide visual references for the observed behaviours. Table 1 additionally provides the overall proportion of individuals that expressed each behaviour at least once during the study period.



37

38 Figure S2: Example images displaying 'Maintenance' behaviours in ruffs during early ontogeny. The birds were
 39 housed first in a box (days 3-9) and later in a larger room (days 11-15). A) Foraging, B) Carrying object, C) Drinking,
 40 D) Defecation, E) In water bath and Bathing (water baths were only available in the larger room), F) Preening, G)
 41 Head Scratching, H) Self-pecking (ring/leg), I) Shaking body parts, here wings and head, J) Shaking head, K)
 42 Stretching extremities, here wing and leg, L) Yawning.

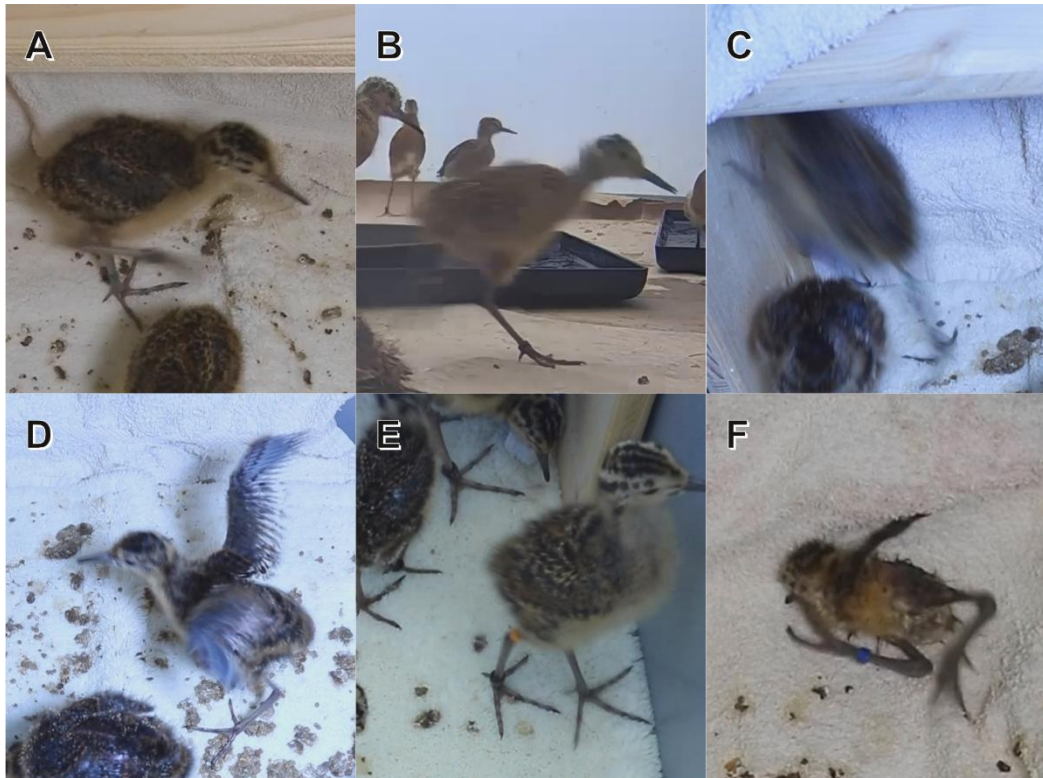


Figure S3: Example images displaying 'Movement' behaviours in ruffs during early ontogeny. The birds were housed first in a box (days 3-9) and later in a larger room (days 11-15). A) Walking (in contrast to other behaviours coded second-by-second instead of frame-by-frame, coded only in the box housing type), B) Running, C) Jumping, D) Flapping wings, E) Stereotypic behaviour, F) Uncoordinated behaviour.

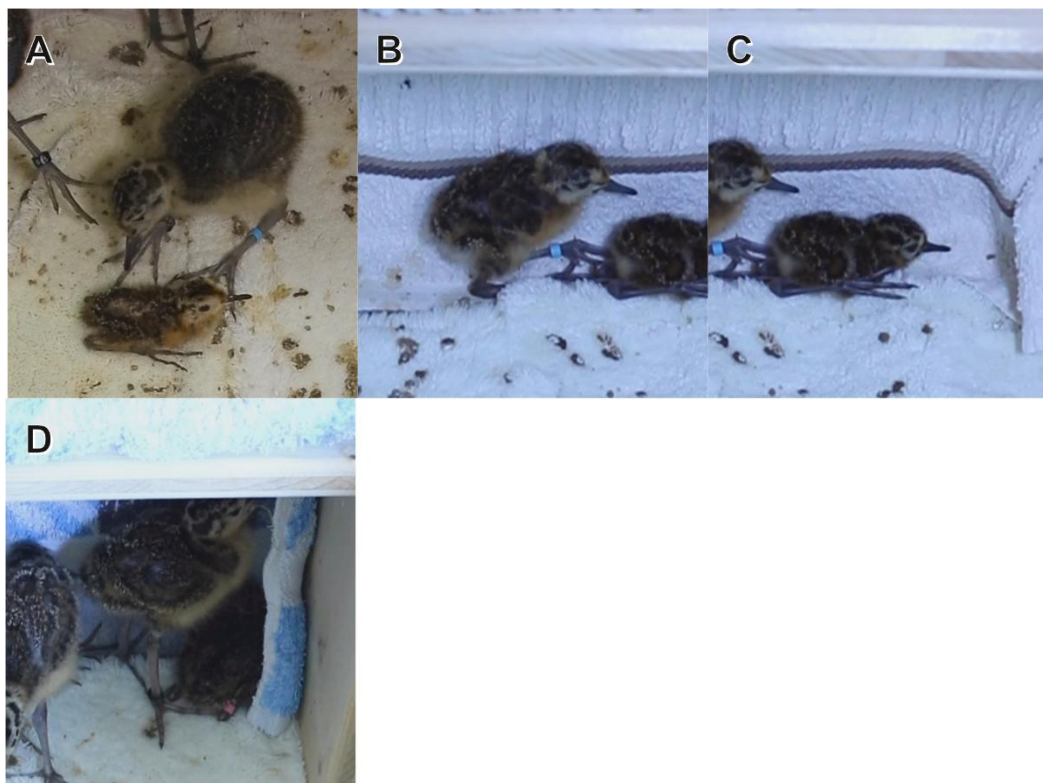


Figure S4: Example images displaying 'stationary behaviour' in ruffs during early ontogeny. The birds were housed first in a box (days 3-9) and later in a larger room (days 11-15). A) Sitting near dummy, B) Sitting elsewhere, C) Crouching, D) Staying frozen (chick standing in the middle).

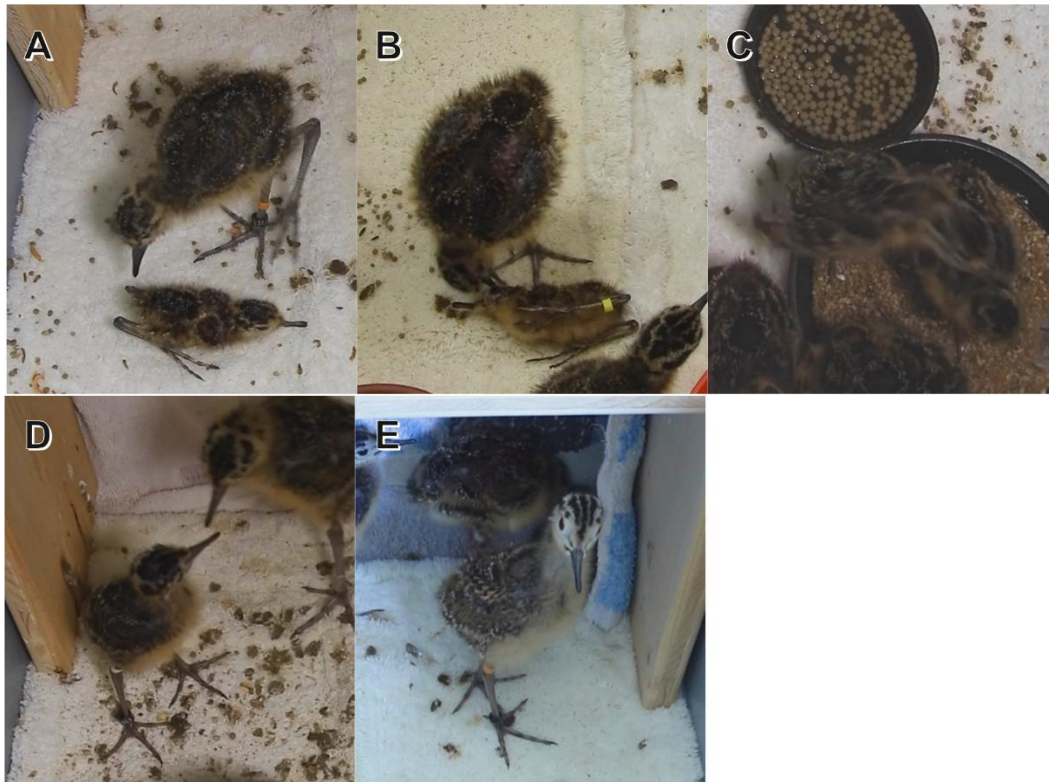


Figure S5: Example images displaying 'Social, Non-sexual' behaviours in ruffs during early ontogeny. The birds were housed first in a box (days 3-9) and later in a larger room (days 11-15). A) Visitation, B) Pecking or touching, C) Aggressive pecking, D) Avoidance (left chick), E) Alertness (in contrast to other behaviours coded second-by-second instead of frame-by-frame, coded only in the box housing type).

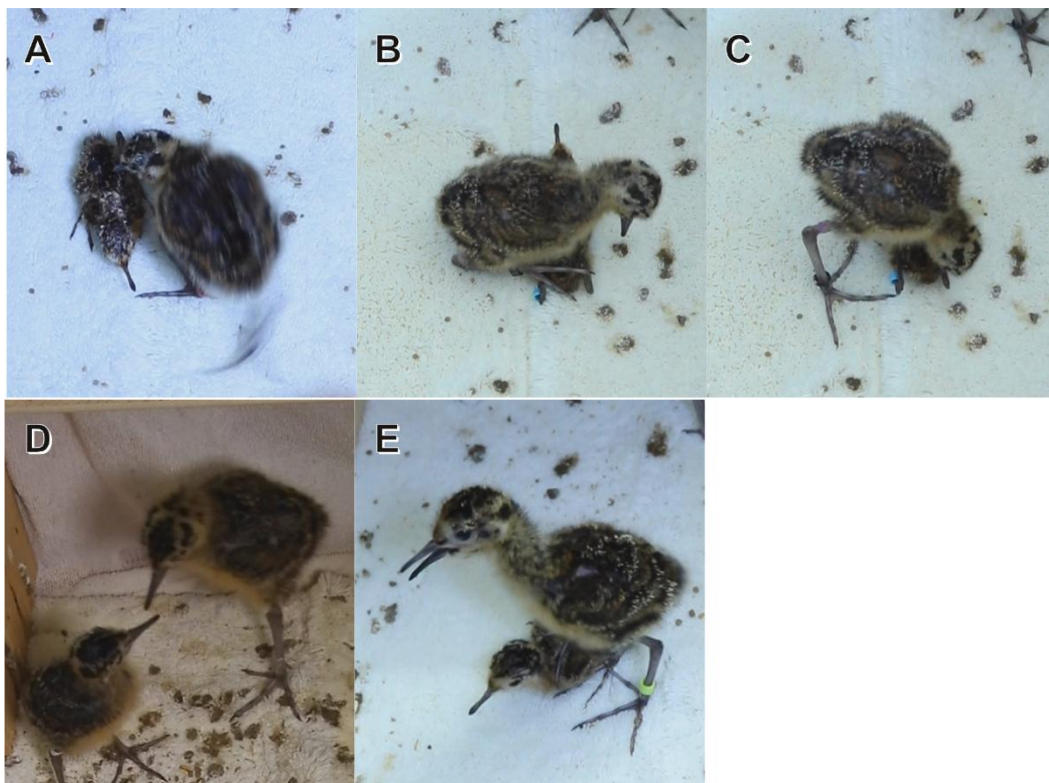


Figure S6: Example images displaying 'Social, Precocious Sexual behaviours' in ruffs during early ontogeny. The birds were housed first in a box (days 3-9) and later in a larger room (days 11-15). A) Circling, B) Mounting, C) Mounting attempt, D) Strutting (right chick), E) Silent cackle.

61 Table S1: Complete ethogram of all behaviours observed in ruff chicks during early development (age: 3 days to
62 15 days) - Overall proportion of individuals showing the behaviour during the whole study period and index of
63 example clip names. The videos are stored in the Edmond repository (<https://doi.org/10.17617/3.7PIHZQ>).

Category	Behaviour	Overall proportion	Name of Example clip
Maintenance	Foraging	1.00	foraging-chicks_food_bowl.MP4
	Carrying object	0.25	carrying_object-orange_ring.MP4
	Drinking	1.00	drinking-red_bowl.MP4; drinking-closest_chick.MP4
	Defecation	0.96	defecation-dark_green_ring.MP4; defecation-pink_ring.MP4
	In water bath	0.86	in_water_bath.MP4
	Bathing	0.08	bathing-front_in_water.MP4
	Preening	0.92	preening-middle_chick.MP4; preening-light_green_ring.MP4
	Head scratching	0.92	scratching-light_green_ring.MP4
	Self-pecking (ring/leg)	0.29	self_peck-white_ring.MP4
	Shaking body parts	0.96	shake_leg-orange_ring.MP4; shake_body-right_chick.MP4
	Head shaking	1.00	shake_head-pink_chick.MP4
	Stretching extremities	1.00	stretch_wing-white_ring.MP4; stretch_wing_leg-far_chick.MP4
	Yawning	0.33	yawning-middle_chick.MP4
Movement	Walking	1.00	walking-dark_green_ring.MP4
	Running	0.79	running-pink_ring.MP4
	Jumping	0.21	jumping-dark_green_ring.MP4
	Flapping wings	0.83	flapping_wings-orange_ring.MP4; flapping_wings-red_ring.MP4
	Stereotypic behaviour	0.42	stereotypic-orange_ring.MP4; stereotypic-dark_green_ring.MP4
	Uncoordinated behaviour	0.58	uncoordinated-dark_blue_ring.MP4
Stationary behaviour	Sitting near dummy	0.38	sitting_dummy-light_blue_ring.MP4
	Sitting elsewhere	0.46	sitting_elsewhere-light_blue_ring.MP4
	Crouching	0.38	crouching-next_to_light_blue_ring.MP4
	Staying frozen	0.21	frozen-all_but_front_chick.MP4

64

65

Category	Behaviour	Overall proportion	Name of Example clip
Social - Non-sexual Behaviour	Visitation	1.00	visitation-orange_ring.MP4; visitation_pecking-red_ring.MP4
	Pecking or touching	1.00	visitation_pecking-red_ring.MP4
	Aggressive pecking	0.38	aggressive_pecking-orange_ring.MP4
	Avoidance	0.21	avoidance-white_ring.MP4
	Alertness	1.00	alertness-orange_ring.MP4
Social - Precocious Sexual Behaviour	Circling	0.71	circling-violet_ring.MP4; circling-red_ring.MP4
	Mounting	0.63	mounting-violet_ring.MP4; mounting-white_ring.MP4
	Mounting attempt	0.54	mounting_attempt-violet_ring.MP4
	Strutting	0.25	strutting-violet_ring.MP4; strutting-pink_ring.MP4
	Silent cackle	0.17	silent_cackle-light_green_ring.MP4

67

68 Rule matrix for co-occurrence of behaviours

69 As part of the data cleaning in R (R Core Team 2024), we applied a rule matrix to define which
70 behaviours could, had to, or could not co-occur (Table S2). This ensured consistent handling of
71 overlapping events and prevented double counting of incompatible behaviours. In addition to the
72 behaviours described in the main ethogram (Table 1), the rule matrix includes the behaviour
73 ‘focus_break’. It marks periods when the focal chick lost focus during a ‘visitation’. The duration of
74 ‘focus_break’ was subtracted from the total ‘visitation’ duration during data processing to ensure
75 accurate quantification.

[illegible]

Results Tables – Main analysis

The main statistical analyses were run separately for each behaviour–housing type combination with sufficient sample size (≥ 3 observations). We used hurdle gamma models to test for age effects on both the probability of occurrence and the mean duration of behaviours. Results for each behaviour are summarised in Table S3Table S10. Each table provides model estimates, credible intervals, and notes on model fit. Models that still produced divergent iterations due to a low number of non-zero data points are greyed out and should be interpreted with caution. For interpretational clarity, we transformed the hurdle model estimates by reflecting the predicted means and credible intervals of the fixed effects around zero. This converts the scale from log-odds of zero to log-odds of non-zero behavioural expression. Accordingly, also Figure 1 displays the probability of behaviour occurrence rather than its absence.

Table S3: Predictors of maintenance behaviours – PART 1 – in young ruffs during early ontogeny, separately for the period housed in a box (days 3-9) and in a larger room (days 11-15). Shown are the outputs of the Hurdle Gamma Models based on the time spent displaying the behaviour within the 6-minute test duration of 24 individuals (160 trials). Greyed out models still produced divergent iterations due to low number of non-zero data points and should be interpreted with care. Slope β is given for fixed effects and variance σ^2 for random effects. Credible intervals (CrI) not overlapping zero are marked in bold. Predicted means and CrIs of fixed effects in hurdle part are multiplied by -1 to show log-odds of non-zero values.

	Maintenance - PART 1							
	Carrying object -				Defecation -			
	Foraging - Box	Foraging - Room	Box	Drinking - Box	Drinking - Room	Defecation - Box	Defecation - Room	
	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	
Conditional part								
Fixed effects								
Intercept	1.03 (0.97, 1.09)	0.89 (0.79, 1)	0.01 (-1.33, 1.3)	0.92 (0.82, 1.02)	1.03 (0.92, 1.14)	-1.01 (-1.06, -0.96)	-0.94 (-0.99, -0.89)	
Age	0 (-0.06, 0.05)	0.04 (-0.05, 0.13)	-0.43 (-1.19, 0.38)	0.05 (-0.01, 0.11)	0.04 (-0.05, 0.14)	0 (-0.03, 0.03)	-0.05 (-0.1, -0.01)	
Random effects								
ID - (Intercept)	0.07 (0, 0.16)	0.13 (0.01, 0.27)	0.81 (0.06, 2.53)	0.2 (0.09, 0.31)	0.13 (0.01, 0.28)	0.07 (0.02, 0.12)	0.04 (0, 0.1)	
Zero-inflation part								
Fixed effects								
Intercept	3.76 (2.42, 5.84)	4.97 (2.93, 8.27)	-3.82 (-6.13, -2.39)	1.61 (0.99, 2.38)	3.1 (1.67, 5.44)	-0.05 (-0.55, 0.45)	-0.58 (-1.56, 0.31)	
Age	-1.34 (-2.75, -0.2)	1.13 (-0.77, 3.74)	-1.05 (-2.37, 0.04)	0.56 (0, 1.15)	0.37 (-0.6, 1.48)	-0.13 (-0.56, 0.27)	0.2 (-0.41, 0.82)	
Random effects								
ID - (Intercept)	0.82 (0.03, 2.5)	0.96 (0.04, 2.93)	1.29 (0.07, 3.45)	0.61 (0.03, 1.65)	2.22 (0.27, 5.11)	0.52 (0.02, 1.32)	1.64 (0.37, 3.26)	
Model parameters								
Adapt delta	0.85	0.80	0.99	0.80	0.80	0.80	0.80	
divergent iterations	0	0	39	0	0	0	0	
# non-zero data points	87 (54.4%)	67 (41.9%)	5 (3.1%)	74 (46.3%)	61 (38.1%)	45 (28.1%)	27 (16.9%)	

Table S4: Predictors of maintenance behaviours – PART 2 – in young ruffs during early ontogeny, separately for the period housed in a box (days 3-9) and in a larger room (days 11-15). Shown are the outputs of the Hurdle Gamma Models based on the time spent displaying the behaviour within the 6-minute test duration of 24 individuals (160 trials). Greyed out models still produced divergent iterations due to low number of non-zero data points and should be interpreted with care. Slope β is given for fixed effects and variance σ^2 for random effects. Credible intervals (CrI) not overlapping zero are marked in bold. Predicted means and CrIs of fixed effects in hurdle part are multiplied by -1 to show log-odds of non-zero values.

Maintenance - PART 2						
	In water bath -		Head scratching -		Self-pecking	Self-pecking
	Room	Preening - Box	Preening - Room	Box	(ring/leg) - Box	(ring/leg) - Room
	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)
Conditional part						
Fixed effects						
Intercept	1.4 (1.27, 1.53)	0.5 (0.14, 0.85)	0.58 (0.31, 0.86)	0.23 (0.05, 0.4)	0.25 (0.13, 0.39)	0 (-0.63, 0.61)
Age	0.02 (-0.08, 0.11)	-0.21 (-0.47, 0.06)	-0.07 (-0.31, 0.15)	0.03 (-0.13, 0.17)	-0.07 (-0.18, 0.04)	0.03 (-1.71, 1.95)
Random effects						
ID - (Intercept)	0.16 (0.01, 0.31)	0.54 (0.24, 0.92)	0.35 (0.05, 0.66)	0.19 (0.02, 0.4)	0.15 (0.01, 0.34)	1.17 (0.07, 3.84)
Zero-inflation part						
Fixed effects						
Intercept	1.12 (0, 2.47)	-1.33 (-2.14, -0.68)	-0.65 (-1.39, -0.01)	-1.36 (-2.11, -0.72)	-0.99 (-1.67, -0.37)	-3.37 (-4.89, -2.31)
Age	1.65 (0.69, 3.03)	0.07 (-0.46, 0.6)	0.5 (-0.04, 1.09)	0.6 (0.07, 1.17)	0.52 (-0.05, 1.11)	0.24 (-0.76, 1.29)
Random effects						
ID - (Intercept)	2.36 (0.64, 4.91)	0.94 (0.07, 2.08)	0.85 (0.04, 2.13)	0.81 (0.05, 1.93)	0.61 (0.03, 1.66)	2.02 (0.28, 4.49)
Model parameters						
Adapt delta	0.80	0.85	0.85	0.80	0.99	0.99
divergent iterations	0	0	0	0	73	1
# non-zero data points	45 (28.1%)	22 (13.8%)	25 (15.6%)	22 (13.8%)	20 (12.5%)	7 (4.4%)

Table S5: Predictors of maintenance behaviours – PART 3 – in young ruffs during early ontogeny, separately for the period housed in a box (days 3-9) and in a larger room (days 11-15). Shown are the outputs of the Hurdle Gamma Models based on the time spent displaying the behaviour within the 6-minute test duration of 24 individuals (160 trials). Greyed out models still produced divergent iterations due to low number of non-zero data points and should be interpreted with care. Slope β is given for fixed effects and variance σ^2 for random effects. Credible intervals (CrI) not overlapping zero are marked in bold. Predicted means and CrIs of fixed effects in hurdle part are multiplied by -1 to show log-odds of non-zero values.

Maintenance - PART 3						
	Shaking body parts - Box	Shaking body parts - Room	Head shaking - Box	Head shaking - Room	Stretching extremities - Box	Stretching extremities - Room
	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)
Conditional part						
Fixed effects						
Intercept	-0.07 (-0.18, 0.03)	0.05 (-0.07, 0.17)	0.12 (0.04, 0.21)	-0.03 (-0.12, 0.06)	0.42 (0.34, 0.51)	0.44 (0.25, 0.62)
Age	0.06 (-0.04, 0.15)	0.04 (-0.05, 0.13)	0 (-0.06, 0.06)	-0.04 (-0.11, 0.04)	0.05 (-0.03, 0.12)	-0.08 (-0.2, 0.04)
Random effects						
ID - (Intercept)	0.08 (0, 0.21)	0.16 (0.01, 0.33)	0.15 (0.05, 0.25)	0.07 (0, 0.19)	0.07 (0, 0.18)	0.25 (0.02, 0.52)
Zero-inflation part						
Fixed effects						
Intercept	-0.34 (-1.12, 0.37)	-0.06 (-0.63, 0.5)	3.03 (1.97, 4.56)	1.91 (1.03, 3.24)	0.9 (0.36, 1.49)	-0.36 (-1.14, 0.32)
Age	0.7 (0.18, 1.27)	-0.07 (-0.58, 0.43)	-1.1 (-2.15, -0.21)	0.32 (-0.39, 1.08)	0.2 (-0.28, 0.69)	0.03 (-0.52, 0.58)
Random effects						
ID - (Intercept)	1.37 (0.37, 2.58)	0.47 (0.02, 1.34)	0.88 (0.03, 2.49)	1.29 (0.09, 3.13)	0.65 (0.03, 1.63)	1.06 (0.09, 2.46)
Model parameters						
Adapt delta	0.80	0.85	0.90	0.85	0.80	0.99
divergent iterations	0	0	0	0	0	1
# non-zero data points	40 (25.0%)	33 (20.6%)	84 (52.5%)	56 (35.0%)	64 (40.0%)	29 (18.1%)
						7 (4.4%)

Table S6: Predictors of non-social, movement behaviours – PART 1 – in young ruffs during early ontogeny, separately for the period housed in a box (days 3-9) and in a larger room (days 11-15). Shown are the outputs of the Hurdle Gamma Models based on the time spent displaying the behaviour within the 6-minute test duration of 24 individuals (160 trials). Greyed out models still produced divergent iterations due to low number of non-zero data points and should be interpreted with care. Slope β is given for fixed effects and variance σ^2 for random effects. Credible intervals (CrI) not overlapping zero are marked in bold. Predicted means and CrIs of fixed effects in hurdle part are multiplied by -1 to show log-odds of non-zero values.

Movement - PART 1				
	Walking - Box	Running - Room	Jumping - Box	Flapping wings - Room
	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)
Conditional part				
Fixed effects				
Intercept	1.65 (1.61, 1.7)	0.55 (0.3, 0.78)	0.15 (-2.28, 2.18)	0.24 (0.16, 0.31)
Age	0.03 (-0.01, 0.07)	0.05 (-0.11, 0.19)	-0.41 (-1.95, 1.64)	-0.06 (-0.15, 0.05)
Random effects				
ID - (Intercept)	0.04 (0, 0.1)	0.41 (0.16, 0.67)	0.88 (0.03, 3.4)	0.09 (0, 0.24)
Zero-inflation part				
Fixed effects				
Intercept	5.14 (2.94, 8.79)	-0.21 (-0.9, 0.43)	-5.07 (-8.57, -2.81)	-1.37 (-2.16, -0.73)
Age	-2.08 (-4.66, -0.34)	-0.34 (-0.91, 0.19)	1.74 (0.38, 3.63)	0.11 (-0.5, 0.73)
Random effects				
ID - (Intercept)	0.97 (0.03, 3.03)	0.86 (0.05, 2.13)	2.34 (0.31, 5.25)	0.64 (0.03, 1.81)
Model parameters				
Adapt delta	0.85	0.80	0.99	0.99
divergent iterations	0	0	0	0
# non-zero data points	89 (55.6%)	31 (19.4%)	5 (3.1%)	29 (18.1%)
				15 (9.4%)

Table S7: Predictors of non-social, movement behaviours – PART 2 – in young ruffs during early ontogeny, separately for the period housed in a box (days 3-9) and in a larger room (days 11-15). Shown are the outputs of the Hurdle Gamma Models based on the time spent displaying the behaviour within the 6-minute test duration of 24 individuals (160 trials). Greyed out models still produced divergent iterations due to low number of non-zero data points and should be interpreted with care. Slope β is given for fixed effects and variance σ^2 for random effects. Credible intervals (CrI) not overlapping zero are marked in bold. Predicted means and CrIs of fixed effects in hurdle part are multiplied by -1 to show log-odds of non-zero values.

Movement - PART 2					
	Stereotypic	Stereotypic	Uncoordinated	Uncoordinated	
	behaviour - Box	behaviour - Room	behaviour - Box	behaviour - Room	
	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	
Conditional part					
Fixed effects					
Intercept	1.24 (0.89, 1.57)	1.42 (0.96, 1.87)	0.06 (-0.24, 0.33)	-0.5 (-2.43, 1.07)	
Age	-0.04 (-0.3, 0.2)	-0.22 (-0.6, 0.15)	-0.25 (-0.44, -0.02)	0.4 (-1.15, 3.01)	
Random effects					
ID - (Intercept)	0.23 (0.01, 0.66)	0.34 (0.02, 1.02)	0.32 (0.02, 0.68)	0.7 (0.02, 3.02)	
Zero-inflation part					
Fixed effects					
Intercept	-3.32 (-5.54, -1.75)	-2.64 (-4.4, -1.49)	-1.63 (-2.62, -0.85)	-3.63 (-5.87, -2.18)	
Age	1.18 (0.28, 2.28)	-0.49 (-1.43, 0.33)	-0.92 (-1.62, -0.3)	1.27 (0.03, 2.87)	
Random effects					
ID - (Intercept)	2.95 (1.26, 5.62)	1.52 (0.1, 3.63)	1.18 (0.13, 2.47)	0.96 (0.03, 2.89)	
Model parameters					
Adapt delta	0.99	0.99	0.99	0.99	
divergent iterations	0	0	0	68	
# non-zero data points	13 (8.1%)	8 (5.0%)	21 (13.1%)	4 (2.5%)	

Table S8: Predictors of non-social, ‘stationary behaviour’ in young ruffs during early ontogeny, separately for the period housed in a box (days 3-9) and in a larger room (days 11-15). Shown are the outputs of the Hurdle Gamma Models based on the time spent displaying the behaviour within the 6-minute test duration of 24 individuals (160 trials). Greyed out models still produced divergent iterations due to low number of non-zero data points and should be interpreted with care. Slope β is given for fixed effects and variance σ^2 for random effects. Credible intervals (CrI) not overlapping zero are marked in bold. Predicted means and CrIs of fixed effects in hurdle part are multiplied by -1 to show log-odds of non-zero values.

	Stationary behaviour			
	Sitting near	Sitting elsewhere	Staying frozen -	
	dummy - Box	- Box	Crouching - Box	Box
	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)
Conditional part				
Fixed effects				
Intercept	0.75 (0.3, 1.19)	1.08 (0.66, 1.51)	1.52 (1.11, 1.93)	0.3 (-2.06, 2.42)
Age	-0.39 (-0.91, 0.13)	-0.35 (-0.64, -0.03)	0.14 (-0.13, 0.42)	0.59 (-1.11, 2.57)
Random effects				
ID - (Intercept)	0.38 (0.02, 1.03)	0.5 (0.04, 1.03)	0.32 (0.01, 1.02)	1.13 (0.08, 3.17)
Zero-inflation part				
Fixed effects				
Intercept	-2.18 (-3.34, -1.4)	-1.87 (-2.86, -1.16)	-2.19 (-3.41, -1.35)	-3.77 (-5.83, -2.45)
Age	-0.06 (-0.73, 0.59)	0.07 (-0.52, 0.69)	-0.04 (-0.7, 0.61)	1.37 (0.23, 2.87)
Random effects				
ID - (Intercept)	1.03 (0.06, 2.57)	0.96 (0.05, 2.25)	1.2 (0.11, 2.73)	0.81 (0.03, 2.45)
Model parameters				
Adapt delta	0.95	0.99	0.99	0.99
divergent iterations	0	0	0	4
# non-zero data points	12 (7.5%)	15 (9.4%)	13 (8.1%)	5 (3.1%)

Table S9: Predictors of social, non-sexual behaviours in young ruffs during early ontogeny, separately for the period housed in a box (days 3-9) and in a larger room (days 11-15). Shown are the outputs of the Hurdle Gamma Models based on the time spent displaying the behaviour within the 6-minute test duration of 24 individuals (160 trials). Greyed out models still produced divergent iterations due to low number of non-zero data points and should be interpreted with care. Slope β is given for fixed effects and variance σ^2 for random effects. Credible intervals (CrI) not overlapping zero are marked in bold. Predicted means and CrIs of fixed effects in hurdle part are multiplied by -1 to show log-odds of non-zero values.

	Social, Non-sexual Behaviour					
	Visitation - Box	Visitation - Room	Pecking or touching - Box	Pecking or touching - Room	Aggressive pecking - Box	Alertness - Box
	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)
Conditional part						
Fixed effects						
Intercept	0.96 (0.8, 1.11)	0.6 (0.34, 0.84)	0.34 (0.18, 0.49)	0.35 (0, 0.69)	-0.96 (-1.16, -0.74)	1.56 (1.51, 1.62)
Age	0.21 (0.12, 0.31)	-0.05 (-0.22, 0.12)	0.25 (0.14, 0.37)	-0.19 (-0.44, 0.07)	0.09 (-0.11, 0.28)	-0.01 (-0.04, 0.03)
Random effects						
ID - (Intercept)	0.28 (0.08, 0.45)	0.29 (0.03, 0.59)	0.21 (0.02, 0.41)	0.3 (0.01, 0.77)	0.13 (0.01, 0.43)	0.08 (0.01, 0.16)
Zero-inflation part						
Fixed effects						
Intercept	1.35 (0.74, 2.09)	-0.51 (-1.28, 0.16)	0.81 (0.11, 1.64)	-1.37 (-2.54, -0.49)	-2.77 (-3.92, -1.89)	5.32 (3.21, 8.81)
Age	-0.09 (-0.6, 0.4)	-0.01 (-0.56, 0.53)	0.37 (-0.13, 0.91)	0.1 (-0.54, 0.76)	0.54 (-0.28, 1.44)	-1.18 (-3.64, 0.62)
Random effects						
ID - (Intercept)	0.74 (0.05, 1.78)	1.05 (0.08, 2.37)	1.27 (0.23, 2.5)	1.61 (0.31, 3.26)	0.62 (0.02, 1.88)	0.97 (0.04, 3.07)
Model parameters						
Adapt delta	0.80	0.80	0.80	0.85	0.99	0.85
divergent iterations	0	0	0	0	0	0
# non-zero data points	71 (44.4%)	27 (16.9%)	60 (37.5%)	18 (11.3%)	7 (4.4%)	91 (56.9%)

Table S10: Predictors of social, precocial sexual behaviours in young ruffs during early ontogeny, separately for the period housed in a box (days 3-9) and in a larger room (days 11-15). Shown are the outputs of the Hurdle Gamma Models based on the time spent displaying the behaviour within the 6-minute test duration of 24 individuals (160 trials). Greyed out models still produced divergent iterations due to low number of non-zero data points and should be interpreted with care. Slope β is given for fixed effects and variance σ^2 for random effects. Credible intervals (CrI) not overlapping zero are marked in bold. Predicted means and CrIs of fixed effects in hurdle part are multiplied by -1 to show log-odds of non-zero values.

Social, Precocious Sexual Behaviour						
	Mounting attempt					
	Circling - Box	Circling - Room	- Box	Mounting - Box	Strutting - Box	Silent cackle - Box
	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)	β/σ^2 (95% CrI)
Conditional part						
Fixed effects						
Intercept	0.45 (0.28, 0.63)	0.36 (-0.48, 1.21)	0.49 (0.18, 0.78)	0.84 (0.69, 1)	0.26 (-0.12, 0.64)	-1.05 (-1.82, -0.15)
Age	0.04 (-0.15, 0.25)	-0.04 (-0.6, 0.46)	0.26 (-0.03, 0.56)	0.06 (-0.09, 0.22)	0.09 (-0.45, 0.67)	-0.01 (-2.13, 2.09)
Random effects						
ID - (Intercept)	0.1 (0, 0.28)	0.62 (0.04, 1.8)	0.26 (0.01, 0.63)	0.16 (0.01, 0.35)	0.24 (0.01, 0.77)	0.37 (0.01, 1.97)
Zero-inflation part						
Fixed effects						
Intercept	-0.54 (-1.72, 0.53)	-3.08 (-5.19, -1.72)	-1.76 (-2.76, -1.01)	-1.27 (-2.18, -0.58)	-2.9 (-4.14, -1.99)	-3.37 (-4.91, -2.29)
Age	1.36 (0.66, 2.22)	-0.81 (-1.93, 0.12)	0.77 (0.15, 1.47)	0.73 (0.18, 1.35)	0.35 (-0.48, 1.23)	-0.21 (-1.28, 0.81)
Random effects						
ID - (Intercept)	2.36 (1.12, 4.19)	1.7 (0.14, 4.01)	1.06 (0.06, 2.47)	1.12 (0.11, 2.43)	0.7 (0.02, 2.12)	0.8 (0.03, 2.39)
Model parameters						
Adapt delta	0.80	0.99	0.95	0.95	0.99	0.99
divergent iterations	0	2	0	0	1	5
# non-zero data points	40 (25.0%)	7 (4.4%)	18 (11.3%)	25 (15.6%)	6 (3.8%)	4 (2.5%)

Coder reliability analysis – Intraclass Correlation Coefficient

To assess reliability between coders, we calculated intraclass correlation coefficients (ICCs) based on a subset of eight randomly chosen observations, each analysed independently by three coders. ICCs were computed using a two-way agreement model with single measures (model = "twoway", type = "agreement", unit = "single") as implemented in the R package *irr* (version 0.84.1; Gamer 2019). Across the complete dataset, coder similarity was very high (ICC = 0.97, 95% CI: 0.96–0.98). When analysed separately by housing type, the agreement remained similarly high (box trials: ICC = 0.97, 95% CI: 0.96–0.98; room trials: ICC = 0.99, 95% CI: 0.98–1.00). Even the behaviour with the lowest agreement, 'Head shaking', still reached an ICC of 0.48 (95% CI: 0.01–0.86). Full results are shown in Figure S7 and Table S11.

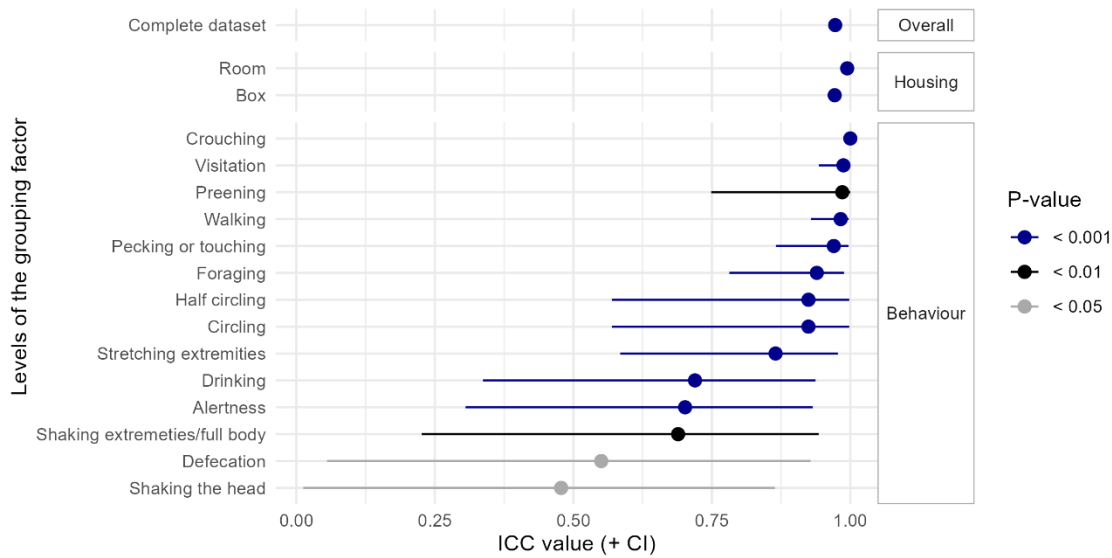


Figure S7: Intraclass Correlation Coefficient (ICC) (model = "twoway", type = "agreement", unit = "single") calculated for a subset of observations (n = 8) coded by all three coders, either across the full dataset ("Overall") or separately within subsets defined by levels of a grouping factor. Note that within this subset of data, only a subset of all possible behaviours occurred often enough in the subset for ICC calculation to be possible.

Table S11: Intraclass Correlation Coefficient (ICC) (model = "twoway", type = "agreement", unit = "single") calculated for a subset of observations (n = 8) coded by all three coders, either across the full dataset ("Overall") or separately within subsets defined by levels of a grouping factor. Note that within this subset of data, only a subset of all possible behaviours occurred often enough in the subset for ICC calculation to be possible.

Grouping factor	Levels of the grouping factor	ICC value (+ CI)	P-value
Overall	Complete dataset	0.97 (0.96, 0.98)	< 0.001
Housing type	Room	0.99 (0.98, 1)	< 0.001
	Box	0.97 (0.96, 0.98)	< 0.001
Maintenance	Preening	0.99 (0.75, 1)	< 0.01
	Foraging	0.94 (0.78, 0.99)	< 0.001
	Stretching extremities	0.87 (0.58, 0.98)	< 0.001
	Drinking	0.72 (0.34, 0.94)	< 0.001
	Shaking body parts	0.69 (0.23, 0.94)	< 0.01
	Defecation	0.55 (0.06, 0.93)	< 0.05
	Head shaking	0.48 (0.01, 0.86)	< 0.05
	Head scratching	-	-
	Self-pecking (ring/leg)	-	-
Movement	Walking	0.98 (0.93, 1)	< 0.001
	Running	-	-
	Stereotypic behaviour	-	-
	Uncoordinated behaviour	-	-
Stationary behaviour	Crouching	1 (1, 1)	< 0.001
	Sitting elsewhere	-	-
	Sitting near dummy	-	-
	Standing in water bowl	-	-
Social - Non-sexual Behaviour	Visitation	0.99 (0.94, 1)	< 0.001
	Pecking or touching	0.97 (0.87, 1)	< 0.001
	Alertness	0.7 (0.31, 0.93)	< 0.001
	Aggressive pecking	-	-
	Avoidance	-	-
Social - Precocious Sexual Behaviour	Circling	0.92 (0.57, 1)	< 0.001
	Mounting attempt	-	-
	Mounting	-	-

References

- Gamer, Matthias (2019): irr: Various Coefficients of Interrater Reliability and Agreement (Version 0.84.1). In *Comput. Softw. Man.*
- R Core Team (2024): R: A Language and Environment for Statistical Computing. Vienna, Austria. Available online at <https://www.R-project.org/>.