

## RESEARCH ARTICLE

# Photoperiod influences the development and the expression of personality traits and social behaviour in wild cavies (*Cavia aperea*)

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## Abstract

Seasonality influences behaviour, physiology and life history of organisms, and photoperiod is a reliable and influential cue gearing individual adaptation to seasonal changes in the environment. Plastic phenotypic adjustments according to the prevailing season are a widespread, well-studied phenomenon. Less well known are effects on developmental trajectories of animals born into different seasons. By manipulating the photoperiod during pregnancy and lactation independent of food availability and temperature, we studied if maternal behaviour in the precocial wild cavy (*Cavia aperea*) responds to this seasonal cue and if maternal behaviour and photoperiod shape offspring development and behaviour. We repeatedly observed mothers before and after birth. We investigated if pups differ in risk-taking behaviours directly after birth (indicating direct prenatal effects) or only after gaining independence of the mother (indicating delayed prenatal or postnatal effects due to own cue sampling). Furthermore, we tested if different simulated seasons of birth affect social and aggressive behaviour of adult animals. While theoretical predictions according to risk-taking are quite clear, they are contradictory for social behaviours that are much less well studied. We predicted that animals born into spring photoperiods would be aggressive because of a need to gather enough resources for early reproduction and successfully establishing a territory at least in males. Spring-born males were more aggressive than autumn-borns, while females did not differ with respect to season. Spring-born females, however, lost more body mass when they had to integrate into an established group and autumn-born females initiated more aggressive interactions. Our data demonstrate flexible and long-term stable seasonal effects on behaviours that likely affect fitness outcomes under natural conditions.

## KEYWORDS

boldness, experimental reproducibility, fearlessness, pace of life, plasticity

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## 1 | INTRODUCTION

Seasonality strongly influences behaviour, physiology and life history of many animal species (Bronson, 1989; Prendergast et al., 2007). In particular, polyoestrous animals need to gear reproductive decisions to the seasonally varying abundance of critical resources because reproduction implies often extreme energy investment (Gittleman & Thompson, 1988; McNamara & Houston, 1996). This makes it important to predict periods of high resource abundance and avoid times when environmental conditions become adverse (Paul et al., 2008). Nontropical rodents born early in the breeding season therefore often undergo rapid reproductive development, thereby enabling reproductive success within their first summer whereas young born later in the season delay reproduction until the next spring (Bronson, 1988; Horton, 2005; Horton & Stetson, 1992; Stetson et al., 1986). Such variation in life history strategies, ranging from slow to fast, is commonly referred to as the pace-of-life (POL, Ricklefs & Wikelski, 2002). According to the POL syndrome hypothesis, within-species differences in the reproductive POL (timing of maturation, emphasis on current vs. future reproduction) should co-vary with behavioural and physiological traits, forming suits of traits optimally adjusted to the environment (Montiglio et al., 2018; Réale et al., 2010). Individuals following a fast POL, i.e. animals born in spring, are therefore expected to develop a bolder, more risk-prone, more aggressive and less social phenotype while individuals following a slow POL should express the opposite traits (Réale et al., 2010). Under natural conditions, this has been found for example in eastern chipmunks (*Tamias striatus*), where individuals of early birth cohorts are faster explorers and start breeding at an earlier age as later birth cohorts (Montiglio et al., 2014). Likewise, bank voles (*Microtus arvalis*) were more active and bolder in spring compared to later seasons (Eccard & Herde, 2013). It remains, however, unclear how such developmental adjustments are brought about, on which cues animals react to adjust the phenotype and whether such adjustments are adaptive or mere results of constraints.

In non-tropical regions, photoperiod is a reliable predictor of seasonal changes and thereby a useful predictive signal used by many species across the animal kingdom to allow adjustment of phenotypic traits and time reproductive investment thereby gearing the life history to resource abundance (Ricklefs & Wikelski, 2002; Tüzün et al., 2021; West & Wood, 2018). In mammals, the environmental signal of day length is converted into a physiological signal by the secretion of melatonin during the absence of light (Goldman & Nelson, 1993). In Siberian hamsters, breeding into long days results in early sexual maturity while breeding into short days delays maturation, even in the absence of any other seasonal cues such as nutrition or temperature (Hoffmann, 1978). Similar effects on fast developmental trajectories in photoperiods indicating spring/summer versus slower development in photoperiods indicating autumn were shown for voles and deer mice (Horton, 1984; Nelson et al., 1997).

The influence of photoperiod on behaviour is less well documented especially when photoperiod is experimentally uncoupled from other seasonally varying cues such as resource availability. Studies on adult rodents show pronounced changes in affective, anxiety-like and aggressive behaviour in response to experimentally altered photoperiods (Nelson & Demas, 1996; Pyter & Nelson, 2006). Recently, a few studies indicate that also the maternal photoperiod during pregnancy (and potentially lactation) has enduring effects on the developmental trajectories of offspring behaviour (Edwards et al., 2021). Siberian hamsters (*Phodopus sungorus*) born and raised into short days develop a more anxious and aggressive phenotype. The maternal photoperiod acts via prenatal melatonin on the developing young to program the offspring for the appropriate seasonal environment the offspring will enter (Edwards et al., 2021; Horton, 2005; Sáenz de Mira et al., 2017).

Such maternally derived cues during the prenatal development may be a reliable predictor of the environment offspring experience after birth if the environment is relatively stable (Fawcett & Frankenhuis, 2015; Kuzawa, 2005). After birth, environmental factors directly influence further offspring development, either integrating with prenatally derived cues if the environment remains stable or alternatively shifting offspring on their developmental trajectories if environmental cues indicate a changed environment (Fawcett & Frankenhuis, 2015). Such postnatal developmental plasticity allows offspring to develop a phenotype optimally geared to the environmental conditions (Bateson et al., 2014).

Among mammals, adjustment in the POL either via natural seasonal variation or via experimentally manipulated photoperiods were so far studied most in altricial rodents and with a strong focus on mainly non-social behavioural traits such as risk-taking and exploration, while social behaviours have largely been neglected (e.g. Adanyia et al., 2021; Rödel & Meyer, 2011; review: Cabrera et al., 2021). We here studied this question in the precocial cavy (*Cavia aperea*) under experimental conditions where we uncoupled food abundance from photoperiod by keeping the food supply ad libitum independent of photoperiod.

The cavy is widely distributed in the temperate/sub-tropical regions of South America. Rood and Weir (1970) reported cavies to reproduce throughout the year in Argentina, except for a short break during midwinter. They also reported a peak of births during spring (August in Argentina). Cavies form social groups of 2–3 females which are monopolised by one dominant male (Asher et al., 2008). Young males not yet large enough to monopolise females migrate after being driven away from their natal group by the dominant male, or they roam around at the territory edges (Asher et al., 2008). From laboratory experiments, we know that exposing pregnant females to increasing photoperiods indicating spring accelerates maturation of males and females while a decreasing photoperiod indicating autumn leads to slower growth and delayed maturation (Guenther, Palme, et al., 2014; Trillmich et al., 2009).

Litter size, litter mass and pup birth mass as well as maternal mass vary seasonally with the lowest values in winter (Rübensam et al., 2015; Trillmich et al., 2019). Similar effects were found under field conditions (Rood & Weir, 1970) and also for the closely related dark-backed cavy (*Cavia magna*; Kraus et al., 2005). Moreover, photoperiod also influenced the behavioural phenotype and the stress response of young individuals after gaining independence from their mother (Finkemeier et al., 2016; Guenther & Trillmich, 2013). In general, animals born into spring-like photoperiods develop a more explorative and risk-prone phenotype (Guenther et al., 2018; Guenther, Finkemeier, & Trillmich, 2014). In addition, animals born into spring-like photoperiods develop elevated levels of natural antibodies and complement activity, have lower resting metabolic rates and lower cortisol baseline concentrations (Guenther et al., 2018; Guenther, Finkemeier, & Trillmich, 2014).

How photoperiod indicative of different seasons affect social behavioural traits is not yet known. We might, however, expect differences in social behaviours due to seasonal fluctuations in social density as observed in many rodent species and therefore the frequency and stability of social interactions and group compositions. Instability of social interactions has already been shown to exert strong and long-lasting changes in social and non-social behaviours in caviaries (Kaiser et al., 2015; Siegeler et al., 2017). If the postnatal photoperiod does not match with the prenatal photoperiod, however, caviaries show high plasticity as they are able to adjust their reproductive and behavioural phenotype with apparently little physiological costs or negative consequences for fitness (Finkemeier et al., 2016; Guenther et al., 2018). Offspring behaviour of caviaries also plastically adjusts to other pre- and postnatal influences such as population density and the stability of the social environment of the mother (Kaiser et al., 2015; Siegeler et al., 2015).

We asked the following specific questions about potential influences of photoperiod on development and expression of behaviour under ad libitum food conditions:

1. Does faster development in spring-borns correspond to behavioural differences between spring- and autumn born pups according to the pace-of-life syndrome hypothesis? Are these behavioural differences present directly after birth or do they develop in early postnatal life, potentially in response to photoperiodic cues directly perceived by the young?
2. Does maternal behaviour differ in increasing (=spring) and decreasing (=autumn) photoperiods and do offspring born into different photoperiods behave differently towards their mother?
3. Once adult, do individuals born in spring or autumn, respectively, differ with respect to social behaviours? Particularly, do they differ in their reaction towards encountering an unknown conspecific? For females, which are the more social sex in this species, we asked whether different photoperiods influence the way they integrate into an existing group of females?
4. In the discussion, we analyse by comparison with earlier experiments in our laboratory how robust such developmental trajectories appear when experiments are repeated under seemingly similar conditions.

## 2 | MATERIAL AND METHODS

### 2.1 | Animals and photoperiodic treatment

We kept the animals in standard enclosures (0.8 m<sup>2</sup>). While breeding, females were kept singly but with acoustical and olfactory contact to conspecifics. After offspring were born, mothers were kept together with their offspring for 19–20 days. The enclosures were located in climate chambers with a constant temperature of 20°C ± 1°C. We prepared each enclosure with wood chips for flooring and a plastic shelter for hiding and resting. The shelter was dark-red and translucent for humans but appeared solid to the animals. Hay, guinea pig pellets (Firma Höveler, Germany) and water were available ad libitum and supplemented with fresh vegetables three times a week. We added Vitamin C to the drinking water once a week (1 g/L).

In Experiment 1, we used 30 multiparous female–male pairs for breeding, of which 29 reproduced successfully. For acclimatization, females were kept under neutral photoperiodic conditions (12L:12D) for 3 weeks. Thereafter, we introduced one male into each enclosure for 4 weeks to ensure successful mating. We started the photoperiodic treatment simulating spring and autumn at the day the males were introduced.

For 15 females, we changed the photoperiod to 10 L:14D when the male was introduced followed by an increase of 15 min more light-time every 9 days (i.e. increasing light time in a single step every 9th day by 15 min), simulating the increasing photoperiod of spring. We chose this light regime as it resembles natural changes in day length in spring in the distribution area of caviaries (30°–35°S; Trillmich et al., 2009). For the other 15 females, again upon introduction of the male, we adjusted the photoperiod to 14.5 L:9.5D followed by a reduction of 15 min light-time every 9 days, simulating autumn photoperiod. When the juveniles were born (2 months after successful mating), both seasonal groups experienced an intermediate photoperiod of 12 ± 0.5 h of light. We checked the enclosures for newborn offspring daily and recorded litter size, individual birth mass and sexes on the day of birth. Each juvenile was marked with a haircut to ensure individual recognition. For the juveniles, the change in photoperiod continued as described above, i.e. for the “spring” group the daily light time increased every 9th day for 15 min until it reached the daylength of a summer day at 35° latitude (14.5 h light), whereas for the “autumn” group daylength decreased further until it reached midwinter daylength (9.5 h light; see Figure 1).

In total, 36 offspring (21 males, 15 females) were born into autumn and 40 offspring were born into spring (24 males, 16 females). We kept the juveniles with their mother and siblings until they were 19–20 days old. At that age, we separated offspring from mothers and kept the young in unrelated same-sex-pairs to prevent breeding. To assess growth from birth to weaning, juveniles were weighed at separation. At separation from the mother, offspring received a pit tag (TROVAN ID-100, passive transponder system; Euro ID, Weilerswist, Germany; dimensions: diameter: 2.12 mm; length 11.5 mm) inserted subcutaneously to ensure permanent recognition.

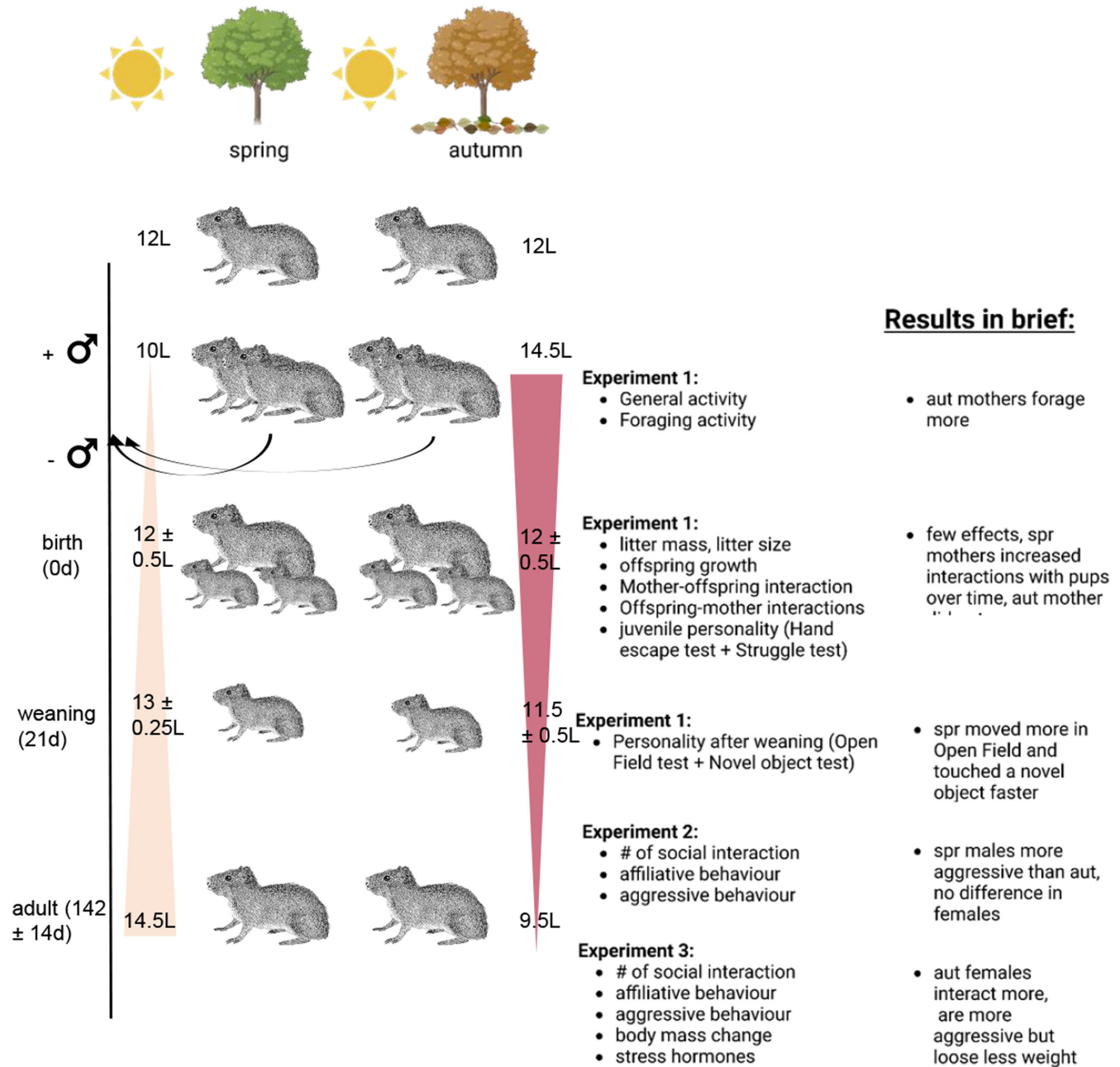


FIGURE 1 Experimental setup overview and results in brief.

When adult, at an age of  $135 \pm 14$  days, animals were moved to larger enclosures ( $1.6 \text{ m}^2$ ). These enclosures were equipped comparably to the enclosures used before but they contained two shelters and could be divided into two equally sized parts by introducing an opaque screen which was used in the social encounter test (Experiment 2; see below). Temperature and feeding regime remained the same as before. After an initial habituation period of 7 days, the social encounter test was conducted twice with a test interval of 7–10 days.

One week after completion of Experiment 2, the females additionally participated in a third Experiment, the social integration test, which lasted 3 days per female. Animals were weighed, and a blood sample was taken for analyses of stress hormone levels before the start of the test and at the end of the test. Thereafter, females

were moved back to their enclosures and kept in the original pairs. The photoperiodic treatment was continued during the whole experiment, thus, spring-born animals conducted the social tests (Experiment 2 and 3) under a photoperiod indicating summer (13:45–13:30h light), while autumn-born animals conducted the social tests under winter-like photoperiods (10:00–10:15h light).

## 2.2 | General experimental procedures

If not mentioned otherwise, all measurements, experiments and video recordings were done at 8–12am or 2–5 pm, corresponding to the activity time of these animals (Guenther, Finkemeier, & Trillmich, 2014; Guenther & Trillmich, 2013).

## 2.3 | Experiment 1: Maternal behaviour and offspring development in spring and autumn

### 2.3.1 | Behaviour of pregnant females in spring and autumn

To investigate whether pregnant females differ in activity and/or feeding patterns in spring and autumn, we video recorded the behaviour of 10 females (5 spring, 5 autumn), three times (each video lasting 1 h) during late pregnancy. We recorded the first video 6 weeks after introducing the male; the following two videos were recorded 1 week apart. At recording days, the animals received fresh food at least 2 h before recording. We recorded the time that females were active versus inactive and the time females spent feeding.

### 2.3.2 | Behavioural Interactions between mothers and offspring

To test if the behaviour of mothers towards their offspring or of offspring towards their mothers differs in spring and autumn, we video recorded the behaviour of all 29 families on the day juveniles were born, and at day 7 and 14 after birth for 1 h each.

We checked enclosures for new-borns daily between 8:00 and 8:30am, so juveniles were at least a couple of hours old before we started recording at 10 am. Cavies are highly precocial, juveniles can walk and run within minutes after birth and even start to eat solid food on their first day of life (Rood, 1972). For easy recognition on videos, we marked each pup with a different colour of finger paint (nontoxic paint which can be easily removed). We recorded the number of times a mother approached one or more of her juveniles and the number of times the mother moved away from her juveniles. In addition, we recorded how often juveniles approached their mother or moved away from her and the time they spent in body contact with the mother.

### 2.3.3 | Development of personality traits before weaning

*Hand-escape test:* We tested offspring a first time when they were three to 4 days old and again at day eight to nine after birth. For this test, we gently removed each pup from the home enclosure and placed it on the open hand of the observer. The hand was then held approximately five centimetres above the ground of the enclosure in such a way that the juvenile did not directly face its mother or siblings. We recorded the latency of each pup to leave the hand (from the moment the hand was introduced to the enclosure to the moment when the pup had left the hand). If it had not left the hand after 60 s, we placed the juvenile back next to its mother and scored "60" as the maximum latency. The procedure did not last more than 2 min. This minimized stress to the juveniles in this early phase of life.

*Struggle test:* We conducted another test at the age of seven to 8 days and again at 12–14 days to measure docility of juveniles. Again,

the test was short to avoid stressing the juveniles. We removed the animal from the home cage and measured for 30 s the time it spent struggling when held on its back in the hand. Afterwards, we placed the animal back into its home enclosure.

### 2.3.4 | Personality after weaning

*Open Field test:* At the age of 21–30 days, we tested fearlessness in an open field, which consisted of a 1m<sup>2</sup> enclosure with a grid drawn on the floor. In the middle of the field, we placed a semi-transparent shelter, which could be lifted out of the enclosure remotely from outside the room. A video camera placed above the set-up recorded the animal's movements for 20 min. We positioned the animal beneath the shelter. For the initial 10 min, we left the shelter in place and the animal had the possibility to explore the open field. Thereafter, we removed the shelter from the enclosure and the animal had another 10 min to explore the field. We recorded the distance covered (in cm) by the animal from the video with the program Labimals (Labimals: analysis of laboratory animals 2008; copyright: H. Bohle and E.T. Krause, Bielefeld, Germany).

*Novel object test:* We tested behaviour in a novel object test, also between 21 and 30 days of age. The test was conducted in the animal's home enclosure after gently removing its partner. We placed the novel object (a 4 cm high green eggcup) in 30 cm distance in front of the shelter, avoiding direct proximity to food and water. We video recorded the animal's interactions with the object for 1 h and measured the latency to the first object contact.

## 2.4 | Experiment 2: Social behaviour of adult offspring in a brief social encounter

The second experiment was conducted using 20 female (10 spring, 10 autumn) and 28 male (14 spring and 14 autumn) animals that were bred in Experiment 1. At this time, the animals were  $142 \pm 14$  days old.

The social encounter test was conducted in the home enclosure of the focal animal. The test arena was created by dividing the home enclosure into two equal sized parts by introducing an opaque screen, confining the focal animal to one half of the enclosure. The second resident animal was gently directed to or placed on the other side of the enclosure. A second, semi-transparent shelter was placed in the middle of the test arena. The shelter gave the animals a possibility to hide during the observation without creating non-observable areas for the experimenter. A stimulus animal was introduced into the test arena and the social interactions initiated by the focal animal were recorded for 15 min immediately after the stimulus animal was introduced.

We used five females and four males as stimulus animals. These animals did not participate in any other experiments. Each test animal conducted the social encounter test twice with a test interval of 7–10 days, once with a male and once with a female stimulus animal. The order in which stimulus animals were presented was randomised.



The experimenter was present in the room in case a social encounter test needed to be interrupted due to severe fighting. This, however, happened only once in this study (trial had to be interrupted after 11 min). The number of total interactions, aggressive, submissive, and affiliative behaviours were recorded for a total of 15 min. Using ethograms based on Rood (1972), aggressive behaviours comprise fixation, demonstrating a curved body posture, chasing, teeth chattering, attacking and biting while submissive behaviour was scored as backing down and evading an aggressive interaction initiated by the stimulus animal. Affiliative behaviours comprise naso-nasal sniffing, naso-anal sniffing, nudging, grooming and resting with body contact.

## 2.5 | Experiment 3: Social Integration of adult female offspring

In the social integration test, we recorded social behaviours of each focal female towards a group of unfamiliar same-sex conspecifics in the home enclosure of this group. Each established group (four groups in total) consisted of four adult females that lived in 2.2 m<sup>2</sup> enclosures equipped with five semi-transparent shelters. The groups were formed about 8 weeks before the focal animals were introduced and hence had plenty of time to establish stable social bonds and a stable hierarchy. No aggression was observed between group members during routine daily checks for at least 2 weeks before the focal females were introduced, indicating a stable social group environment.

Focal females were introduced into one of the four groups randomly between 12:00 and 13:00 h. The focal female stayed in the group for 3 days. Directly after introducing the focal female, social behaviour was recorded using a video camera for 1 h. Three days later, a second video was recorded for 1 h at the same time of day. For easy recognition of the focal female, the female was marked with a stripe of white finger paint on her back. Pilot studies have shown that this treatment does not affect behaviour of the focal animal or group members. Recorded behaviours were the same as in the social encounter test. Behavioural interactions were scored every 30 s. In addition, the time that the focal animal spent close (within one body length) to another group member was measured. Directly before we introduced the females into the groups, and when the test stopped, we measured body mass of focal females to test for the effect of the integration on body mass loss.

### 2.5.1 | Blood sampling and cortisol concentration

We took blood samples of focal females at the start and end of the social integration test to assess the stressfulness of this situation. These samples were taken within 3 min after catching the animal to avoid an increase of cortisol concentration due to disturbance. The ear of the animal was rubbed with a special ointment

(ELACUR, Riemser Arzneimittel AG) to stimulate blood circulation. The animal's marginal ear vein was punctured and about 70 µl of blood were collected. The blood samples were centrifuged for 4 min with 13,000 rpm to separate the plasma. The plasma was then frozen at a temperature of -20°C and analysed in the Department of Behavioural Biology in Münster based on a competitive immunoassay (RE52061 IBL, IBL International GmbH, Hamburg, Germany). The assay used specific antibodies against cortisol (for details of the procedure see: Kaiser et al., 2003; Künzl et al., 2003). The antibody cross-reacted with relevant steroids as follows: prednisolone 29.8%, 11-desoxycortisol 8.48%, cortisone 4.49%, prednisone 2.12%, corticosterone 1.99%, 6b-hydroxycortisol 1.03%. The intra-assay % CV was below 5%.

### 2.5.2 | Statistical analyses

All statistical analyses were conducted using the free software R (R Core Team, 2020). Figures show means ± SE. Activity and feeding duration of pregnant females was analysed using mixed effects models including the seasonal treatment and the video trial as fixed effects and female identity as random effect. Similarly, movements of mothers towards or away from their offspring and movements of offspring to or away from their mother were analysed using mixed effect models. Season, offspring age and their interaction were coded as fixed effects and maternal identity was coded as random effect.

Offspring litter size and litter mass were analysed using a t-test.

Struggle duration and hand escape latency were tested twice in all offspring. Season, sex and trial (1 or 2) and their two-way interactions were coded as fixed effects and offspring identity nested within maternal identity were coded as random effects. To test for repeatability, trial was the only fixed effect used and offspring identity was used as a sole random factor. Confidence intervals based on 1000 bootstrapping and permutation-based *p*-values are derived from the rptR packages (Stoffel et al., 2017). Behavioural tests after weaning, were only conducted once. A similar model structure as before was used with the exception that season and sex were the only fixed effects.

### 2.5.3 | For experiments 2 and 3

To analyse the effects of season on behavioural and hormonal traits, we used univariate linear mixed effects models, fitting season, sex, measurement number and the season:sex interaction as fixed and animal ID as random effect. A Gaussian distribution was assumed in all cases except for the number of aggressive and the number of affiliative interactions for which a Poisson distribution yielded better model fit. In case the season:sex interaction was significant, we split the data set and analysed the effect of season separately for males and females. Model fit for all models used was checked visually using Q-Q plots.

### 3 | RESULTS

#### 3.1 | Experiment 1: Maternal behaviour and offspring development in spring and autumn

##### 3.1.1 | Maternal behaviour

Neither litter sizes nor litter mass differed between seasons with a mean litter size of  $2.7 \pm 0.27$  (litter mass:  $160 \pm 15$  g) in spring and  $2.4 \pm 0.25$  (litter mass:  $158.5 \pm 16.3$  g) in autumn ( $N = 29$ , litter size:  $t = 0.83$ ,  $p = .41$ ; litter mass:  $t = 0.322$ ,  $p = .75$ ). Of the 10 mothers that we tested for patterns of activity and feeding behavior during pregnancy, autumn mothers spent more time feeding compared to mothers in spring conditions ( $N = 10$ ,  $F = -2.2$ ,  $p = .03$ , mean feeding time spring:  $46 \pm 16$  s, autumn:  $162 \pm 41$  s). This effect was independent of number and mass of offspring. There was no difference in general activity ( $F = 0.89$ ,  $p = .37$ ).

##### 3.1.2 | Pup behavioral development

Offspring growth from birth to weaning differed significantly between seasons ( $N = 76$ , treatment:  $t = -2.39$ ,  $p = .023$ ), with autumn-born offspring growing faster than spring-born offspring (weaning mass  $212 \pm 36$  g and  $193 \pm 23$  g, respectively). Also, males grew about 10% faster than females (sex:  $t = 2.47$ ,  $p = .016$ ), but the interaction between season and sex was non-significant. There was no statistical difference in the amount of time mothers and their offspring spent together in different seasons with spring families spending on average 26 min together during the 1 h recording and autumn families spending on average 31 min together ( $F = 0.50$ ,  $p = .48$ ). There was no difference in the amount of time spent together across the three recordings, ranging from on average 28 min on day 1 to 25 min on the day 14 recording ( $F = 0.84$ ,  $p = .36$ ). Spring mothers and their offspring tended to spend less time together with increasing age of pups compared to autumn mothers ( $F = 2.74$ ,  $p = .099$ ). Autumn

mothers showed no change in the number of approaches to their offspring across age while spring mothers more than doubled their approaches to pups from the day of birth to day 14, leading to a significant interaction of time and age ( $F = 4.03$ ,  $p = .05$ , Figure 2). There was no such pattern and no overall treatment difference in the number of movements away from their pups. Movements of offspring away from their mother increased with age ( $F = 29.1$ ,  $p < .001$ , Figure 2) but did not differ between season ( $F = 1.76$ ,  $p = .19$ ) or sex ( $1.32$ ,  $p = .25$ ). The number of movements towards the mother, however, were more frequent in young born in autumn ( $F = 4.9$ ,  $p = .03$ , Figure 2) but showed no sex effect ( $F = 0.13$ ,  $p = .75$ ) and no treatment-specific pattern over time ( $F = 2.6$ ,  $p = .10$ ).

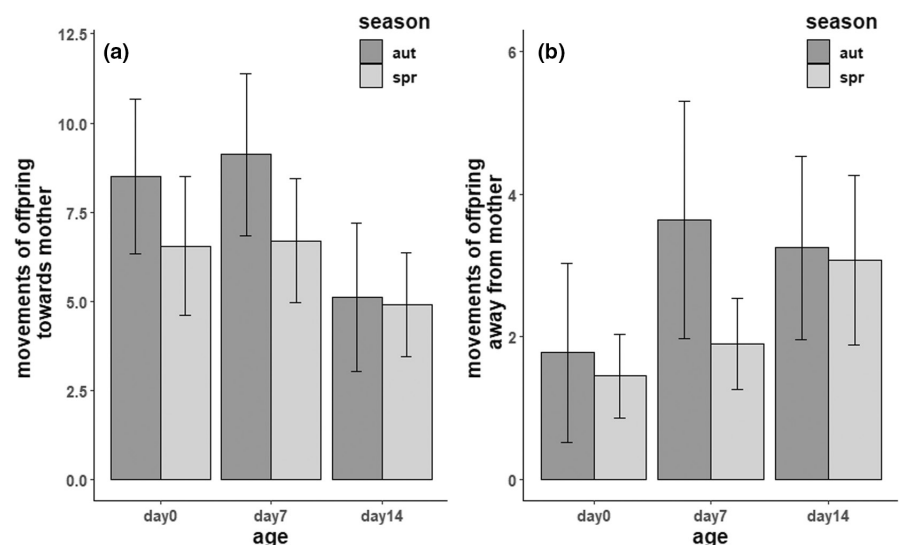
Offspring showed lower latencies in the hand-escape test and struggled more as they grew older. This pattern was not significantly different between seasons (means  $\pm$  SE;  $N = 76$ , hand-escape test, age:  $t = -2.3$ ,  $p = .02$ ; season:  $t = -0.5$ ,  $p = .62$ ; struggle test, age:  $t = 4.32$ ,  $p < .001$ ; season:  $t = -0.14$ ,  $p = .9$ , Figure 3).

##### 3.1.3 | Behaviour of young after weaning

After weaning, offspring born in different seasons clearly differed in the personality tests. Spring-born offspring moved more in the open field (independent of sex) than autumn-born young (season:  $N = 71$ ,  $t = 2.7$ ,  $p = .01$ , Figure 4) and touched a novel object faster ( $N = 71$ , season:  $t = -2.8$ ,  $p < .01$ , Figure 4). A significant interaction of season and sex ( $t = 2.35$ ,  $p = .02$ ) was found in the novel object test, with female offspring reacting differently to a novel object, depending on season. Spring-born females were the fastest to approach a novel object.

#### 3.2 | Experiment 2: Social behaviour of adult offspring in a brief social encounter

In the social encounter test, the animals were fully adult ( $142 \pm 14$  days; mean  $\pm$  SE) and sexually mature. With on average



**FIGURE 2** Behaviour of offspring towards their mother. (a) number of movements towards the mother and (b) number of movements away from the mother.

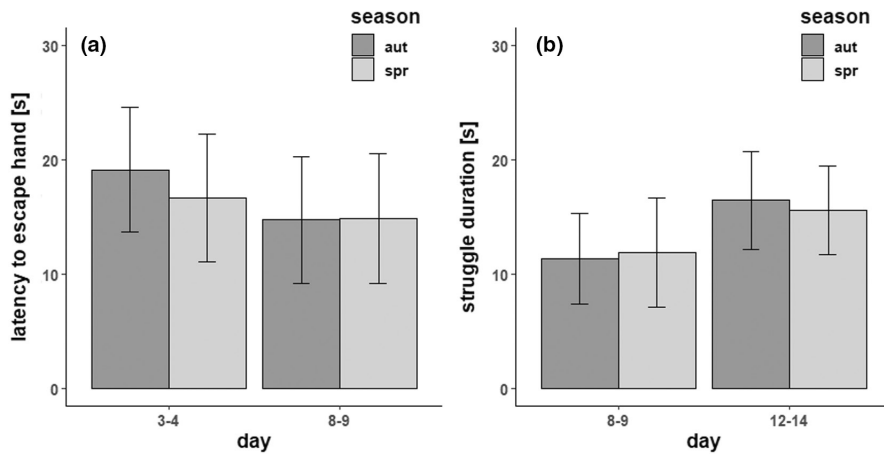


FIGURE 3 Stress-coping behaviour of non-independent juveniles.

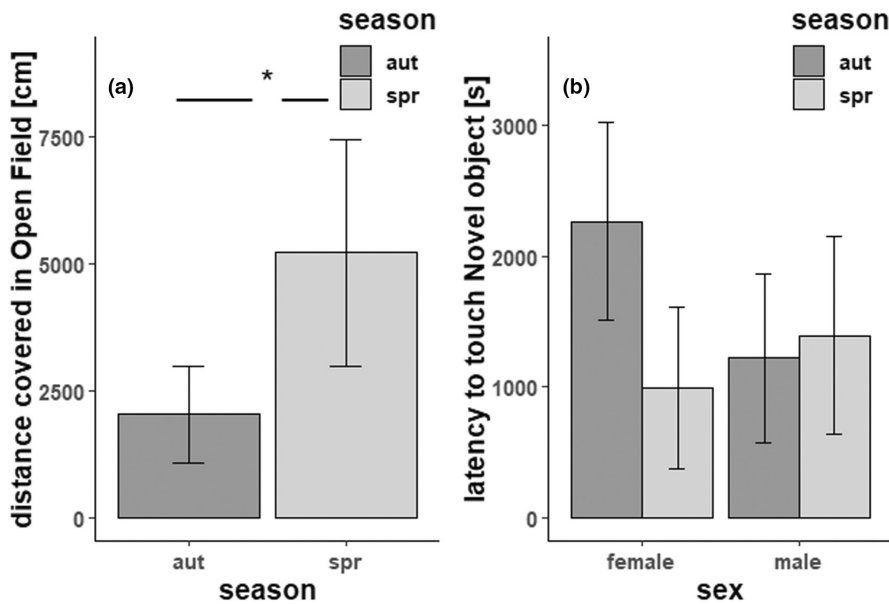


FIGURE 4 Behaviour of juveniles around weaning in open field and novel object tests.

$11 \pm 1.5$  interactions, there was no significant difference in the number of total interactions ( $t = -0.88$ ,  $p = .38$ ) or the number of affiliative interactions (average:  $3.2 \pm 0.4$ ;  $t = 0.24$ ,  $p = .82$ ) between animals born into different seasons. Males interacted less often with the stimulus animals than females ( $f: 15.6$ ,  $m: 10.5$ ,  $t = -3.5$ ,  $p = .001$ ) but there was no sex difference in the number of affiliative interactions. For aggressive interactions, there was a significant interaction between season and sex ( $t = 2.04$ ,  $p = .04$ , Figure 5). While spring born males showed more aggressive interactions than autumn born males ( $t = 2.4$ ,  $p = .02$ , Figure 5), there was no seasonal difference in females ( $t = -0.90$ ,  $p = .38$ , Figure 5). In the second test 7–10 days later, the tendencies to interact proved repeatable (Table 1).

### 3.3 | Experiment 3: Social Integration of adult female offspring

At an age of  $145 \pm 15$  days, for females only, we tested if there were seasonal differences in how they integrated into an existing group with a stable rank hierarchy. On average, females spent  $7.3 \pm 2.0$  min

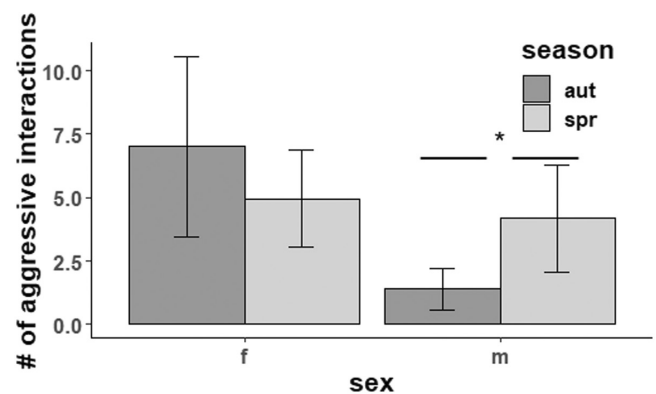


FIGURE 5 Number of aggressive interactions/15 min initiated by males and females born in different seasons in the social encounter test. Shown are means  $\pm$  SE.

close to group members during both video recordings without statistically significant changes between measurement times or between seasons. The timing (day 1 vs. day 3) also did not influence any of the other variables significantly. The number of total interactions



TABLE 1 Repeatability estimated from intercept only models

Variable	Repeatability (CI)	p-value
Experiment 1		
Struggle duration	0.47 (0.26–0.64)	.001
Hand escape latency	0.46 (0.27–0.63)	.001
Experiment 2		
# interactions social encounter	0.33 (0.06–0.58)	.01
# aggressive interactions social encounter	0.69 (0.5–0.82)	<.001
# affiliative interactions social encounter	0.40 (0.14–0.60)	.002

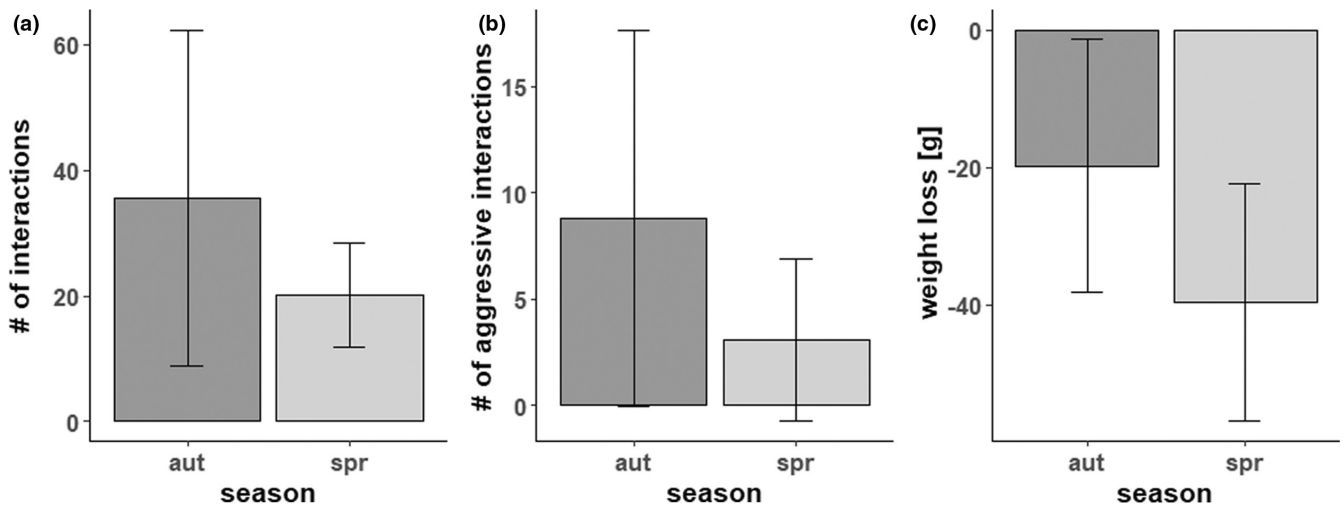


FIGURE 6 Behaviour of females in the social integration test. (a) Autumn born females initiated more interactions with other group members in total. (b) Autumn born females initiated more aggressive interactions. (c) Autumn-born females lost less body weight during the 3 days of social integration. Shown are means  $\pm$  SE.

( $t = 3.41$ ,  $p = .003$ , Figure 6a) as well as the number of aggressive interactions ( $t = 2.6$ ,  $p = .01$ , Figure 6b) were both elevated in autumn born females, while the number of affiliative interactions did not differ between animals grown up in different seasons.

On average, females lost about 5% of body mass during the 3 days of the group integration test. Females born into autumn lost only about half as much weight during the test compared to females born into spring ( $t = 3.4$ ,  $p = .002$ , Figure 6c). There was no seasonal difference in the increase of cortisol during the test ( $t = -0.43$ ,  $p = .67$ ). Baseline cortisol values were  $1294 \pm 125$  ng/mL and tested females of both groups showed a strong increase of on average  $1329.6 \pm 308$  ng/mL (103%) in cortisol concentrations after 3 days ( $t = 2.26$ ,  $p = .03$ ).

## 4 | DISCUSSION

In adult animals, cues offered by photoperiod may lead to phenotypic adjustments in behavior and physiology that prepare the animal for predictably different challenges of the spring/summer and the autumn/winter season. This phenotypic flexibility (*sensu* Stamps & Groothuis, 2010) has been well documented for aggressive behavior which often increases during the winter season when food

resources likely become limited and competition may become high (Jasnow et al., 2002; Rendon et al., 2017).

We here studied behavioural developmental phenotypic plasticity of juveniles in response to photoperiod in the cavy, a highly precocial species that reproduces multiple times within a year to determine whether such adjustments occur and are adaptive with respect to POL. We considered developmental aspects and explicitly tested whether photoperiodic adjustment also affects social behaviour of adults born under different photoperiods, an aspect that has so far received little attention.

### 4.1 | Developmental differences induced by photoperiod

Our first question concerned whether pups born under a spring photoperiod develop a faster pace of life and corresponding risk-prone behavioural phenotype as expected according to the pace-of-life syndrome hypothesis. Given the highly precocial nature of cavy pups we wondered whether these behavioural differences were present immediately after birth or develop potentially in response to photoperiodic cues directly perceived by the growing young?

Growth of animals born into spring and autumn photoperiod differed clearly. Contrary to our expectation, autumn born young grew faster before weaning. This deviates from earlier findings (see Table 2 for a summary of present and previous findings). All of these experiments were run using the same manipulation of photoperiod under the same feeding conditions as used in our present experiment. This suggests that growth rate of pups until weaning is a variable trait that depends substantially on factors other than photoperiod, like maternal size and condition (Kasparian et al., 2005; Trillmich et al., 2019).

Before weaning, we found no differences in behavioural traits between offspring born under spring and autumn photoperiod conditions. However, soon after weaning, young born in autumn photoperiod moved less in the Open Field (OF; were less fearless) and had a higher latency to approach and touch a Novel Object (NO; were less bold) than young born in spring. For the Open Field and Novel Object results, this agrees with earlier findings (see Table 2).

Struggle and hand escape test appear to measure the same behavioural trait as the Open Field test, as shown by Guenther and Trillmich (2015). However, the former tests are much faster and presumably less stressing than an Open Field test for very young animals and using different tests within a short time period as done here avoids habituation effects. Higher fearlessness and boldness of spring animals as displayed through faster exploration in the OF and shorter latency to approach and touch the NO could be interpreted as an indication of a more active coping style. This may help the spring born animals to explore and establish faster in their environment in correlation with earlier reproduction (Finkemeier et al., 2016). The differences in behaviour that we observed after weaning between spring and autumn born animals indicate a tendency for a faster behavioural POL of the spring animals although early growth rates appear to show the opposite pattern.

Differences in the development of behavioural traits after birth became obvious only after weaning indicating substantial plasticity of the postnatal developmental trajectory. Similarly, when testing over longer time spans, changes in behavioural traits during development have also been found in American red squirrels (*Tamiasciurus hudsonicus*; Kelley et al., 2015) where activity and aggression scores regressed towards the mean as animals aged. In rats, Rödel and Meyer (2011) observed changes in personality traits before and after weaning that depended on litter size. Herde and Eccard (2013) similarly documented major changes in behavioural traits over ontogeny in common voles (*Microtus arvalis*). In birds, Würz and Krüger (2015) found substantial changes in behavioural traits in the Zebra finch (*Taeniopygia castanotis*) across ontogeny and Class and Brommer (2015) showed the same in the blue tit (*Cyanistes caeruleus*). Thus, developmental plasticity appears to be a quite general characteristic in shaping personality traits.

As Fawcett and Frankenhuis (2015) have pointed out, plastic adjustments during development are theoretically expected given a degree of uncertainty about the environment and the extent to which experiences during ontogeny provide useful cues about future conditions. Major environmental changes in an animal's state during ontogeny can lead to shifts in the kind of interactions with conspecifics and many aspects of the environment. As a consequence, it

appears adaptive to restructure specific behavioural traits as well as their correlations with each other (Cabrera et al., 2021; Guenther, Finkemeier, & Trillmich, 2014). We here show that seasonal changes constitute one such major environmental factor inducing plastic adjustment of personality traits across ontogeny.

## 4.2 | Does photoperiod induce differences in social behavior?

Secondly, we focused in our study on social behavior in early life interactions between mothers and their offspring and potential influences of the photoperiod experienced early in life on adult social behavior. Changes in pup behavior in response to photoperiod experienced by the mother during pregnancy or by themselves shortly after birth represent developmental plasticity. On the other hand, differences in adult behavior in response to photoperiod are often described as adaptive, regularly reversible seasonal phenotypic flexibility (Groothuis & Trillmich, 2011; Stamps & Groothuis, 2010) of behavioural traits. This applies here for the maternal behavior. All females initially came from a similar natural photoperiod but were then exposed to different experimental manipulation of photoperiod throughout pregnancy. In our reproducing cavy, females photoperiod alone - without the natural seasonal differences in resource abundance - induced differences in maternal feeding time, but not in activity. Mothers approached young in their litters less frequently in autumn than in spring and, as is to be expected, somewhat compensatorily, young in autumn litters approached their mothers more frequently than those in spring litters. Our observations may indicate the adult's tendency to get herself into optimal condition for the winter leading to a slightly lower motivation of mothers to care for autumn offspring. It may also relate to the finding that in outdoor conditions litters of autumn pups tend to be smaller but individual pups heavier than those born in spring (Rübensam et al., 2015; Trillmich et al., 2019). We found a similar pattern here, even though in our sample it was not statistically significant. The larger size at birth of autumn pups may - under natural conditions - lead to even faster independence of the highly precocial young or ensure that they quickly gain sufficient energy resources to overcome food shortage and low temperatures.

Depending on sex, cavies born in autumn photoperiod differed from those born in spring when tested as adults for social behaviour. In the 15-min Social Interaction Test, males born in autumn proved less aggressive than those born in spring whereas females did not differ. In the Integration Test lasting 3 days, the autumn born females interacted more and also behaved more aggressive than those born in spring, but autumn born animals lost less body mass during the 3 days than spring borns. Whether these differences can be interpreted to indicate that males in autumn are less motivated to establish a territory (Asher et al., 2008) whereas females are more under pressure to establish in a site with sufficient resources remains speculative. Cortisol levels increased strongly in the Integration Test indicating a major activation by the adjustment to new social conditions during integration into the unknown groups of females.

**TABLE 2** Summary of findings from this and earlier studies. ad, adult; spr, simulated spring photoperiod; aut, simulated autumn photoperiod; HE, hand escape test; ST, struggle test; LF, Long field (exploration); NO, Novel Object (boldness); OF, Open Field (fearlessness); NA, not measured. Time is given as hh.min, L, light, D, dark. Photoperiod used: stable means no further change in L:D; continuing changes indicates L:D changing every 9th day as described in the Method section. Age at testing is generally given in days; 'adult' means the animals are fully grown (at least 6–8 months old).

Publication	Sex	Photoperiod	Test age (days)	Growth to weaning	Behaviour	RMR	Hormones	Traits scored
This study	ad ♀♀	Continuing changes in photoperiod	Fully adult	NA	spr mothers < time feeding than aut mothers	NA	NA	Activity, time feeding
This study	♀♀ & ♂♂, early ontogeny	Continuing changes in photoperiod	7–14 (before weaning) 21–30 (after weaning)	spr < aut	♀ & ♂ spr = aut in docility before weaning; spr ♀ > aut ♀ in fearlessness after weaning; ♂spr = aut ♂ in fearlessness	NA	NA	HE, ST, NO, OF
This study	same ♀♀ & ♂♂ as adults	Continuing changes in photoperiod	142	NA	spr ♂ > aggressive than aut ♂; spr = aut in ♀	NA	NA	Social interaction
This study	same ♀♀ as adults	Continuing changes in photoperiod	145	NA	spr > aggressive but lost > mass than aut	NA	NA	Social integration
Guenther & Trillmich (2013)	♀♀ & ♂♂	Continuing changes in photoperiod	22–30	spr = aut	♀: spr more bold, explorative & fearless than aut. ♂ spr = aut	♀ trend: spr > aut ♂ spr = aut	NA	LF, NO, OF
Guenther, Palme et al. (2014)	♂♂	Continuing changes in photoperiod	0, 45 (80,120)	spr = aut;	NA	NA	spr earlier than aut increase in testosterone	Growth; testosterone
Guenther, Finkemeier, & Trillmich (2014)	♀♀ & ♂♂	Continuing changes in photoperiod	20–21 (75–110)	spr = aut	spr = aut	spr > aut	spr = aut basal CORT	RMR, basal Cort, LF, NO, OF
Finkemeier et al. (2016)	♀♀ & ♂♂	Changes in photoperiod until day 35 <sup>a</sup>	20–35	spr = aut	spr bolder, more explorative & tend to be more fearless than aut	Trend: spr > aut	NA	RMR, growth LF, NO, OF
Guenther et al. (2018)	♀♀ & ♂♂	Continuing changes in photoperiod	25–30	spr = aut	spr bolder, more fearless and docile than aut	NA	NA	Growth, NO, OF, ST
Guenther et al. (2021)	♀♀	Changes in photoperiod until day 22 <sup>a</sup>	18–22	spr = aut	spr bolder than aut	spr = aut	NA	RMR, growth, NO

<sup>a</sup>The further experiments in this study were match-mismatch experiments (with respect to photoperiod) and were therefore not included here.

The Cortisol responsiveness was similar to that observed during a 2-h isolation period in an enclosure without shelter in guinea pigs (Ryström et al., 2022). Somewhat surprisingly, there was no difference in the increase in Cortisol level in the spring and autumn groups despite marked differences in weight loss. Thus, we found a number of substantial differences in social behavior of the mature animals between those born in spring and autumn. That such behavioral differences especially in social behaviours can be adaptive has been demonstrated for guinea pigs which have to adjust to different social conditions (Guenther, Kowalski, & von Engelhardt, 2014; Zimmermann et al., 2016). Zimmermann et al. (2016) showed that males housed during adolescence together with a female behaved more aggressive and attained a dominant position against adolescent males housed in colonies where they had adjusted to a subdominant role. Likewise, Guenther, Kowalski, and von Engelhardt (2014) showed that sons of mothers housed under low density situations during pregnancy, such as often observed in spring, were more aggressive, obtained dominant positions and had higher reproductive success in a competitive reproductive situation.

Adanyia et al. (2021) observed that Siberian hamsters (*Phodopus sungorus*) differed in social behavior before and after maturation and, following Cabrera et al. (2021) who found no consistency in sociality, suggested that social behaviours are less stable than non-social behaviours (in their case escape behavior). However, they only tested social behavior once after maturation, so that it remains unclear, how repeatable it was after maturity.

Our findings and those of other authors suggest high flexibility and consequent low repeatability of social behaviour in adult animals. However, the potential importance of seasonal changes has often not sufficiently been taken into account and many studies – like our own with respect to the Integration Test – have not explicitly tested the repeatability of social behaviour after maturation. This suggests that it would be valuable to study the extent of phenotypic plasticity in social behaviour in more species and in much more detail than has so far been done.

### 4.3 | Robustness of repeated experimental outcomes

When we compare our results reported here with earlier findings from the same laboratory (see Table 2), using the same breeding stock and essentially the same methods largely implemented by the same experimenters it becomes obvious that the details of the early ontogeny described here and in earlier publications are surprisingly labile. Comparable to earlier studies (Guenther et al., 2018, 2021 but see Guenther, Finkemeier, & Trillmich, 2014), we found spring born animals to be bolder and more active stress copers after weaning. However, Guenther and Trillmich (2013) did not find such differences. In the current study, behavioural differences were not present in stress-coping traits before weaning, suggesting that they emerge slowly post-natally as a consequence of direct exposure to the photoperiod or a late expressed maternal effect. Given the

variable outcomes of different experiments done by the same authors as described above, it may quite generally be more useful to compare the directions of such effects and effect sizes rather than focussing on the significance of differences which to some extent is arbitrary given the chosen significance threshold.

On the other hand, for example, in earlier experiments heavier females in a given litter born into autumn photoperiod were less explorative but lighter females within a litter showed no such difference related to photoperiod (Guenther & Trillmich, 2015). These authors also found no difference in the behaviour of males with respect to photoperiod. Furthermore, Guenther, Finkemeier, and Trillmich (2014) found no effect of photoperiodic treatment on the personality type expressed by juvenile animals.

In our experiments, we always determined the sample size necessary to achieve clear results by power analysis based on the effect sizes seen for age at maturity as observed by Trillmich et al. (2009). For the series of experiments conducted across 10 years, we thus have seven sets on experimental animals with highly comparable number of breeding pairs (ranging from 28–33 breeding pairs for each experiment). However, given the potentially confounding effects of litter size (see also Rödel & Meyer, 2011), maternal age and condition etc. estimated required sample sizes may still be too low. Unavoidably, assumptions about the mentioned factors that may influence the experiments have to be made and these hidden assumptions cannot completely be taken into account in a power analysis. Moreover, developmental plasticity apparently can lead to labile effects. Consequently, we would recommend to increase required sample size substantially above those required by power analysis to achieve robust results.

Testing age also appears to play an even more important role than often assumed when investigating the development of personality traits: In the above mentioned paper (Guenther et al., 2018) animals were tested when 25–30 days of age, in Guenther et al. (2021) when 18–19 days old. Whether these slight differences in age can account for the different results remains to be determined, but it may hint at an unexpectedly large influence of the age at testing on the outcome. To our knowledge, there is no other comparable series of experiments investigating photoperiodic effects or developmental aspects of personality traits in general under so closely comparable conditions. Thus, our results either suggest a high lability in the outcome of repeated experiments even under closely similar conditions within the same laboratory or an unexpectedly high influence of test age and other factors usually unaccounted for. Our series of what we considered very comparable experiments but with sometimes slightly different outcomes, support recent calls for taking action to achieve better reproducibility in science (e.g. Held & Schwab, 2020) by using replicated studies and right from the start planning larger sample sizes than required by simple power analysis.

### AUTHOR CONTRIBUTIONS

**Anja Guenther:** Conceptualization; Investigation; Writing - original draft; Writing - review & editing; Visualization; Methodology.  
**Fritz Trillmich:** Conceptualization; Writing - original draft; Writing - review & editing; Project administration; Resources.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

The raw data associated with this article have been uploaded to the data server of Bielefeld University and will be publicly available under doi: <https://doi.org/10.4119/unibi/2964040>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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