



Integrating behaviour, physiology and survival to explore the outcome of reintroductions: a case study of grey partridge



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ARTICLE INFO

Article history:

Received 15 January 2020

Initial acceptance 14 April 2020

Final acceptance 1 March 2021

MS number: 20-00037R

Keywords:

behaviour
coping style
corticosterone
Cox survival model
grey partridge
personality
physiology
reintroduction
state behaviour feedback
survival

Personalities, i.e. consistent individual differences in behaviour, have been found in many animal populations. However, the reasons why personalities emerge, how they persist and the consequences they have in a changing environment are poorly understood. Factors influencing personalities include genetic background, prenatal (e.g. hormonal) and postnatal (e.g. environmental) conditions, and the strength of these factors can affect the consistency of personalities over time, and hence their flexibility in a changing environment. In birds, for example, hormones in eggs deposited by mothers can modulate aggressiveness of offspring and environmentally induced nutrition deficits in offspring can reduce neophobia later in life. Hence, investigating the fitness consequences of personalities requires the integration of physiological, behavioural and survival measures. We used the opportunity of a reintroduction project of grey partridge, *Perdix perdix*, to experimentally explore how multiple pre- and postnatal factors including measures of the hormone corticosterone were related to three behavioural traits. Then, we investigated whether the behaviours were repeatable and related to survival after release into the wild. Grey partridges showed distinct personalities affected by multiple pre- and postnatal factors. Proactive birds had low baseline levels of circulating corticosterone and survived longer after release into the wild compared to reactive and passive personalities. Consequently, the number of survivors after 6 months was substantially higher for proactive than for reactive and passive birds. Integrating data on behaviour, physiology and survival thus allows the investigation of the complex interplay of personality and fitness in a changing environment.

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Behavioural traits are often correlated within individuals across time and environmental contexts, resulting in consistent behavioural differences between individuals (i.e. personalities; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). Variation in personalities are part of the phenotypic variability within populations and can be subject to natural selection (Dammhahn, Dingemanse, Niemelä, & Réale, 2018; Dingemanse, Both, Drent, & Tinbergen, 2004; Smith & Blumstein, 2007).

Three of several interacting factors that can shape personalities are genetic background, prenatal parental environment and postnatal environmental conditions (Groothuis & Trillmich, 2011).

Depending on the strength of these three factors, personalities might be consistent or labile throughout life (Groothuis & Trillmich, 2011; Smith & Blumstein, 2012; van Oers, Klunder, & Drent, 2005). A few factors, such as pleiotropic genes, could maintain consistent personalities over the lifetime of an individual (Dochtermann & Dingemanse, 2013; Ketterson & Nolan, 1999; Sih et al., 2004). Alternatively, multiple independent pre- and postnatal factors could govern behaviour throughout life and allow for flexible adjustments according to environmental context or life history stage (Sih et al., 2004; Wilson, 1998).

Behavioural traits are partly heritable and candidate genes orchestrating behaviour are known (Thomson, Watts, Pottinger, & Sneddon, 2011; van Oers & Jong, 2005). Strong correlations of genes and behaviour imply that personalities are very consistent over time and environmental contexts, which allows organisms to quickly respond to selection (Sih et al., 2004; Van Schaik, 2013). However, strong correlations of genes and behaviour can also entail poor behavioural flexibility and result in maladaptive behaviours

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such as hyperaggression towards mates (Chang & Sih, 2013; Smith & Blumstein, 2012).

Birds offer excellent opportunities to study the relationships between genes, prenatal and postnatal environment, personality and fitness (van Oers & Jong, 2005). In birds prenatal conditions and parental effects can affect personalities directly through information transfer via eggs (Henriksen, Rettenbacher, & Groothuis, 2011), or through mediators such as body size at hatching (Mayer, Shine, & Brown, 2016). For example, in black-headed gulls, *Chroicocephalus ridibundus*, high concentrations of egg androgens boosted aggressiveness of offspring, which probably supported territoriality and productivity of offspring in adulthood (Eising, 2006). Maternal effects can be passive responses to environmental factors, or mothers can actively adapt and prepare the offspring for the environment she experienced before or during egg laying (Love & Williams, 2008; Mousseau & Fox, 1998).

Various postnatal factors can affect avian personalities transiently or permanently, allowing for quick adjustments according to context (Sih et al., 2015). For example, micronutritional deficiencies during sexual maturation reduced neophobic behaviours in zebra finches, *Taeniopygia guttata*, which suggests that these personality traits have a sensitive window during adolescent development (Kim, Noguera, Morales, & Velando, 2010). Avian personalities can also remain responsive to environmental cues throughout life. Female Ural owls, *Strix uralensis*, raising chicks defended their nests more fiercely and produced more recruits when vole densities in their environment were high (Kontiaainen et al., 2009).

Short-term modulations of behaviour can be associated with intrinsic factors such as levels of glucocorticoids in birds and mammals. As summarized in proactive–reactive coping styles (Koolhaas et al., 1999), proactive personalities exhibit relatively low levels of glucocorticoids whereas these levels are relatively high in reactive, passive and shy individuals (Carere, Caramaschi, & Fawcett, 2010; Koolhaas et al., 1999). State–behaviour feedbacks can stabilize personalities (Niemelä & Dingemans, 2018). For instance, a predator attack can elicit a startle response in its prey which drives up circulating glucocorticoids. In turn, high glucocorticoids can elicit and sustain a passive and shy personality type in the prey (Koolhaas, Boer, Coppens, & Buwalda, 2010; Sih et al., 2015).

Ultimately, different personality types prevail under fluctuating selection pressures (Dingemans et al., 2004; Smith & Blumstein, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007). Importantly, personalities well adapted to one set of environmental conditions can struggle under a different selection regime. For example, in great tits, *Parus major*, slow-exploring males and fast-exploring females tended to survive better in years with low winter food availability whereas the inverse pattern was evident when winter food was plentiful (Dingemans et al., 2004). Relationships between personality and fitness are hard to study under natural conditions due to the many factors involved. Animal reintroductions offer good opportunities to study these relationships because (genetic) origin, prenatal parental environment and the postnatal environmental conditions before release can be controlled. Behaviour and physiology can be measured in captivity and related to fitness after release (Dingemans et al., 2004; Fisher, James, Rodríguez-Muñoz, & Tregenza, 2015). This approach allows the exploration of the proximate causes and the wider consequences of personalities. It might also enable personalities to be chosen for release that suit the postrelease environment (Bremner-Harrison, Prodhon, & Elwood, 2004; Haage, Maran, Bergvall, Elmhagen, & Angerbjörn, 2016; Merrick & Koprowski, 2017; Smith & Blumstein, 2012).

For our study, we participated in a reintroduction project of grey partridges in Switzerland which used recent descendants of wild birds and birds bred in captivity for more than 30 generations ('domesticated'; see Methods for details). Birds of these two strains were subjected to predictable or unpredictable prenatal and postnatal feeding thereby creating eight experimental groups (two strains times two prenatal times two postnatal feeding schemes). We analysed data on physiology, behaviour and postrelease survival with three main aims. First, we investigated how strain, perinatal feeding schemes and plasma corticosterone concentrations (CORT) affected behaviour taking genetic relatedness and social group assignment into account. Second, we analysed whether the three behavioural traits representing proactive, reactive and passive behaviour were repeatable and correlated. Finally, we explored whether distinct behavioural types showed differences in survival after release into the wild.

In earlier studies, we found effects of strain and feeding schemes on physiology (Homberger, Jenni-Eiermann, Roulin, & Jenni, 2013; Jenni et al., 2015) and survival (Homberger, Jenni, Duplain, Lanz, & Schaub, 2014). Here, we focused on impacts of strain and feeding schemes on behaviour and its fitness consequences. In accordance with the literature on proactive–reactive coping styles (Coppens, Boer, & Koolhaas, 2010; Koolhaas et al., 1999) we expected that domesticated strain birds would show rather proactive personalities associated with their low glucocorticoid stress response whereas wild strain birds would have high glucocorticoid stress responses and rather reactive personalities (Homberger et al., 2013; Homberger, Jenni-Eiermann, & Jenni, 2015). Prenatal and postnatal food availability could affect personalities of the two strains in complex manners (Kim et al., 2010; Kontiaainen et al., 2009). Finally, we predicted that proactive personalities could experience a selective advantage in the unknown postrelease environment due to their explorative nature (Smith & Blumstein, 2007).

METHODS

Origin of Birds

The grey partridge is a ground-dwelling wildfowl species which has drastically declined throughout Europe (Kuijper, Oosterveld, & Wymenga, 2010). In Switzerland, it became virtually extinct in the 1990s. For a reintroduction programme, we imported grey partridge eggs from a U.K. breeder (Perdix Wildlife Solutions, Stratford-upon-Avon, U.K.) and released full-grown birds that hatched from these eggs in 2009 and 2010. Parents producing eggs originated from two strains. Male and female grey partridges of the first strain were captured from a sustainable wild population in eastern England. The following spring, female offspring from these wild pairs were mated with males captured in the wild and offspring of this semiwild strain produced eggs for our study. These birds were considered genetically close to the wild population (subsequently called wild). Parents of the second strain were from a population kept and bred in captivity for at least 30 generations without adding new birds (subsequently called domesticated) and had thus probably adapted to captivity (Homberger et al., 2013). In 2009 22 parental pairs (11 of each strain) and in 2010 50 parental pairs (25 of each strain) produced eggs. Offspring of the two strains differed in physiology (Homberger et al., 2013) and genetics (Jenni-Eiermann, Jenni, Olano Marin, & Homberger, 2019).

Experimental Procedure

We used a crossed-design experiment subjecting parents of both strains and their offspring to predictable or unpredictable feeding schemes. Parental housing, egg production and prenatal

feeding schemes were conducted at the breeder's premises in the U.K. When the mating season started, birds were allowed to freely choose their mate from the covey with which they spent the winter and were then kept in pairs. During oviposition (April to May) parents were either subjected to a predictable feeding scheme with ad libitum access to food (called prenatal predictable feeding; five pairs per strain in 2009 and 12 pairs per strain in 2010) or access to food was denied during an unpredictable 4 h time window between 0800 and 2000 each day (six and 13 pairs per strain; prenatal unpredictable feeding). Eggs were collected daily, transported to Switzerland weekly and artificially incubated. On the hatching day, chicks were individually marked and assigned to coveys, i.e. social groups, of approximately 32 birds (seven to eight birds per strain \times prenatal treatment combination). Coveys were housed in indoor aviaries (200 \times 80 cm and 80 cm high) during the subsequent 4 weeks. In the first week after hatching, all birds had ad libitum access to food and water.

Starting from the second week, half of the indoor aviary groups were maintained on the predictable feeding scheme (food ad libitum), whereas the second half was subjected to the postnatal unpredictable feeding scheme (food withdrawn for 3–4 h per day at unpredictable times). All chicks received standardized food (Trutenküken Vormast, Kliba-Nafag, Kaiseraugst, Switzerland).

At 29 days old, birds were relocated into outdoor aviaries (8 \times 4 m and 2 m high) that resembled the species' natural habitat including grassy vegetation, hide-aways and sandbathing opportunities. After the postnatal treatment phase (age 44 days in 2009, age 29 days in 2010), birds were assigned to new outdoor aviary coveys consisting of approximately 32 birds (i.e. four birds per strain \times prenatal \times postnatal treatment combination). These new coveys remained together until release and received food and water ad libitum throughout the rest of the time in the aviaries.

Behavioural Tests

When the birds were 44 (2009) or 52 (2010) days old, we performed three behavioural tests to obtain a single measure of a maximum of 392 birds of the eight strain \times prenatal \times postnatal treatment combinations (exact sample sizes are given in the tables and figures). To investigate whether behavioural traits were consistent over time, we repeated the same three tests six times in a subsample of 47 birds from three coveys and 15 parental pairs between July and November 2009. These three coveys were not released and provided no data to the survival analysis, but they were kept under the same conditions as the coveys bound for release. Repeated tests were conducted between 33 and 121 days of age with 8–25 days between test repeats.

The three behavioural tests were conducted consecutively between 0800 and 1400 in the order presented below. During the tests, birds had no visual contact with the experimenter or, except for the separation test, with conspecifics. Test aviaries were similar to home aviaries but had sun and rain protection. Tests lasted for a maximum of 10 min. If a bird did not react within 10 min it was assigned a test time of 600 s. The proportions of birds that were assigned 600 s are given in [Appendix Fig. A1](#).

First, an emergence test was conducted to measure proactivity, that is, the motivation to venture into a new environment in an isolated context ([Davis, Schmidt, & Doescher, 2008](#); [Forkman, Boissy, Meunier-Salaün, Canali, & Jones, 2007](#)). One bird was put into a wooden box (80 \times 40 cm and 20 cm high) which was placed in the test aviary. After acclimatization for 5 min, the front sliding door of the box was opened remotely and the bird's latency to fully emerge from the box was measured. Emergence can be interpreted as a proactive behaviour since it is self-initiated rather than a reaction to a direct stimulus ([Koolhaas et al., 2010](#)).

Second, we measured tonic immobility which can be considered a reactive antipredator response ([Forkman et al., 2007](#); [Miyatake, Nakayama, Nishi, & Nakajima, 2009](#)). To induce tonic immobility, the bird was gently restrained in a supine position on a wooden table by covering its feet and sternum with one hand and the head with the other hand. After 10 s the hands were withdrawn, and the time it took the bird to recover from tonic immobility was measured. We were able to induce tonic immobility in all birds.

Finally, a separation test was conducted to measure activity in a social context or the urge for social reinstatement ([Faure & Mills, 2014](#); [Réale et al., 2007](#)). One bird was put into a wooden box (80 \times 40 cm and 20 cm high) which was placed in the test aviary. After acclimatization for 5 min, the front sliding door of the box was opened remotely; the bird then had visual contact with a mixed-sex group of conspecifics placed 6 m away in a compartment at the other end of the test aviary. We measured the time it took the bird to approach, to within 10 cm, the compartment of conspecifics. The urge for social reinstatement can be interpreted as a reactive behaviour since it is a direct stimulus reaction to the presence of the conspecifics ([Koolhaas et al., 2010](#)).

Blood Sampling and Determination of Plasma Corticosterone Levels

Blood samples were taken 1 day after the behavioural tests at an age of 45 days in 2009 and 4 days after the behavioural tests at an age of 56 days in 2010. Blood sampling consisted of randomly capturing birds from their home aviary and obtaining a drop of blood collected with a capillary tube within 3 min after first disturbance to determine baseline plasma CORT levels ([Romero & Reed, 2005](#)). We obtained blood samples within 3 min after approaching the aviary with a well-trained group of assistants. After the bird was held in an opaque cotton bag, a second blood sample was taken 30 min after first disturbance to measure stress-induced CORT levels. After blood sampling the birds were measured (tarsus, body mass) and returned to their home aviaries. Blood samples were chilled immediately after sampling and centrifuged within 2 h. Plasma samples were stored at -20°C until laboratory analysis.

To measure plasma CORT, we used an enzyme immunoassay (for details see [Müller et al., 2007](#)). CORT was extracted from plasma using 4 ml dichloromethane and incubated overnight in the presence of an antibody (Chemicon, Limburg an der Lahn, Germany; cross reactivity: 11-dehydrocorticosterone 0.35%, progesterone 0.004%, 18-hydroxydeoxycorticosterone 0.01%, cortisol 0.12%, 18-hydroxycorticosterone 0.02% and aldosterone 0.06%). An HRP-corticosterone complex served as enzyme label and ABTS [2,2'-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid)] as substrate. Samples were evaluated in triplicates. Inter- and intra-assay coefficients of variance were 3.0% and 22.1%, respectively.

Radiotagging and Release of Birds

At approximately 110 days old, a subsample of 177 birds was equipped with 11 g necklace radiotransmitters with a mortality switch (RI-2BM; Holohil Systems Ltd., Carp, ON, Canada) in due consideration of the Guideline for the Reintroduction of Galliformes for Conservation Purpose ([IUCN, 2009](#)). Releases took place 1 week after tagging between mid-September and mid-November in the southwest of Switzerland (6°04'E, 46°15'N). Release procedures are described in detail elsewhere ([Homberger et al., 2014](#)). After release, the state (alive or dead) of each radiotagged individual was recorded at least once per week throughout the 9-month observation period using Yagi antennas (Titely Electronics Ltd, Ballina, Australia) and digital receivers (R1000 of Communications Specialists Inc., Orange, CA, U.S.A. and SIKA of Biotrack,

Dorset, U.K.). After release, birds typically remained in their coveys and did not disperse over large distances making false-positive death recordings due to dispersal outside of the detection area very unlikely. Since we used radiotransmitters with a mortality switch which change their pulse frequency when the tag is not moved for 24 h, we could determine date of death (and often even the cause of death) accurately. We collected most tags in the field and could distinguish between true death events and lost/stripped-off tags based on marks on the tags or remnants of a carcass close by.

Data Analysis

The analyses are based on two data sets. The first included one measure of emergence, tonic immobility and separation (sample sizes are given in the tables and figures) of each individual (single-measure data set). A subsample included measures of CORT and survival (number of days survived after release). This single-measure data set was used to (1) analyse which factors affected the behavioural traits taking into consideration parent ID and ID of the covey in the outdoor aviary; (2) evaluate relationships between the three behavioural traits; (3) analyse relationships between behaviour and survival. The second data set included the six repeated measures of each behavioural test of 47 individuals in three coveys from 15 parental pairs (repeated-measures data set). In addition to parental origin and covey effects, the repeated-measures data set allowed us to estimate the variance among individuals and among test dates (individual and date-specific consistency of behaviour).

Survival and behaviour measures were right censored since observation of survival was restricted to 9 months although some individuals were still alive after this time. Likewise, behavioural measures stopped after 600 s although some birds had not yet shown the respective behaviour (see [Appendix Figs. A1 and A2](#)).

To analyse factors affecting single behavioural traits, measures of behavioural tests were treated as time-to-event data (time until the bird showed the respective behaviour) and analysed using Cox mixed-effects models (Ripatti & Palmgren, 2000; Therneau, Grambsch, & Pankratz, 2003) in the statistical software R (R Core Team, 2018). Cox mixed-effects models account for the right censoring of the dependent variables. The exponent of their fixed effects gives the hazard ratio (HR), that is, the proportional change of an event probability. The exponent of the standard deviation of the random effects indicates the average variation of the HR for this random effect (Pankratz, Andrade, & Therneau, 2005). We defined three full models (one for each behavioural test) using the single-measure data set. The full models included baseline or stress response CORT levels, the main effects and interactions of strain and perinatal feeding schemes and sex, body mass, year and test date as explanatory variables ([Appendix Table A1](#)). For the repeated-measures analysis, we defined three full models with sex, linear and quadratic test date as fixed factors and parent ID, covey ID, individual ID and test date as random factors. Nonsignificant variables were consecutively eliminated from the full models until only the main terms of strain and perinatal feeding and significant terms remained. The relationships between the behavioural traits were analysed using an agglomerative clustering procedure (two-step clustering in SPSS 18) with a log-likelihood similarity measure and the Akaike information criterion as the criterion to determine the number of clusters. The silhouette measure of cohesion and separation was > 0.5, indicating clustering.

Survival was analysed using all birds that had undergone all three behavioural tests and were equipped with radiotransmitters (177 birds). Both the dependent variable survival (time until

Table 1
Estimates of the Cox mixed-effects models for the analysis of the three behavioural test measures as obtained from the single-measure data set

	Emergence			Tonic immobility			Separation		
	HR	± SE	P	HR	± SE	P	HR	± SE	P
Fixed effects									
Strain (wild)	1.039	0.841	0.870	0.867	0.744	0.91	0.995	0.848	0.966
Prenatal food supply (unpredictable)	1.012	0.819	0.980	0.854	0.735	0.91	0.830	0.707	0.243
Postnatal food supply (unpredictable)	0.901	0.782	0.42	0.939	0.824	0.22	1.165	1.019	0.255
Corticosterone baseline	0.977	0.967	0.013	0.981	0.974	0.049	1.004	1.001	NS
Corticosterone stress response ¹	1.002	0.999	0.57	0.998	0.995	0.20	0.733	0.641	0.021
Sex (male)			NS			NS			NS
Body mass			NS	1.912	1.512	6.82	6.592	3.715	10.29
Year (2010)			NS	1.025	1.018	13.33			NS
Test date			NS						NS
Test date squared			NS						NS
Strain*perinatal treatment			NS						NS
Strain*postnatal treatment			NS						NS
Prenatal*postnatal treatment			NS						NS
Strain*perinatal*postnatal treatment			NS						NS
Random effects									
Parents	SD = 0.55	exp(SD) = 1.73	<0.001	SD = 0.25	exp(SD) = 1.29	1.58	SD = 0.34	exp(SD) = 1.41	7.87
Covey	SD = 0.65	exp(SD) = 1.92	<0.001	SD = 0.39	exp(SD) = 1.47	14.24	SD = 0.99	exp(SD) = 2.69	116.9

The models of the emergence and tonic immobility tests included 321 individuals of 62 parental pairs and 22 coveys. The separation test included 338 individuals of 22 coveys and 66 parental pairs. Parent ID and covey ID were included as random effects in all analyses. The hazard ratio (HR) for continuous variables indicates the change in the occurrence probability per unit change in the explanatory variable. HR > 1 indicates a relatively higher and HR < 1 a relatively lower probability of occurrence of the behaviour. NS = nonsignificant variables that were removed from the full model (see [Appendix Table A1](#) for the full model).

¹ Coefficients and statistics for corticosterone stress response when included as a predictor instead of baseline corticosterone.

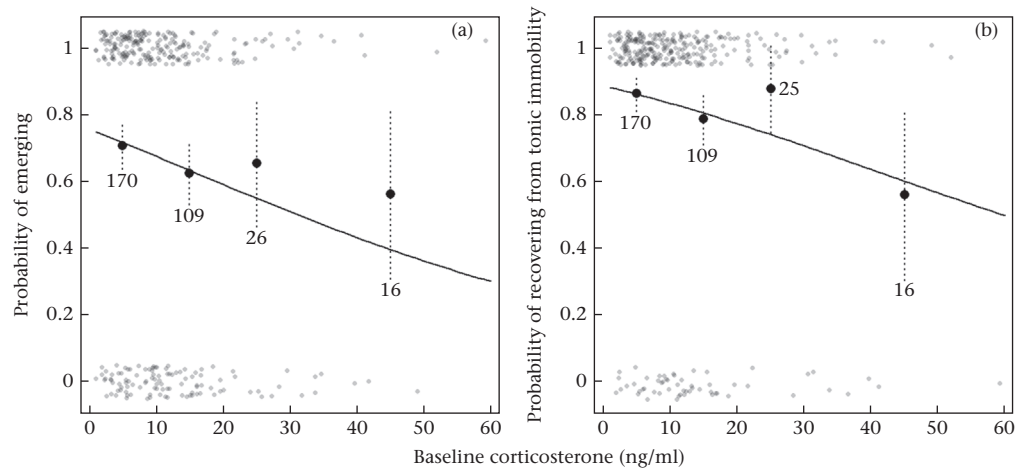


Figure 1. Relationship between baseline CORT and (a) the probability of emerging and (b) the probability of recovering from tonic immobility. Lines indicate the predicted relationship from the final models of emergence and tonic immobility (see Table 1). Semitransparent dots indicate for each individual whether behaviour occurred (dots scattered around 1) or not (dots scattered around 0). Solid dots with 95% confidence intervals and sample sizes are mean occurrence probabilities for four ranges of CORT (0–10, 11–20, 21–30, 31–60 ng/ml) according to the raw data.

death) and the explanatory behavioural variables (time until the bird showed the respective behaviour) were censored. To account for censoring of survival and behavioural measures, we fitted Cox mixed-effects models (Clayton, 1994) using MCMC sampling in WinBUGS (Lunn, Thomas, Best, & Spiegelhalter, 2000). The behavioural measures were assumed to be exponentially distributed: $x_i \sim \text{Exponential}(\lambda)I(c_i+)$, where x_i is either the time measured until the behaviour was observed or a missing value (NA) if the behaviour did not occur within 600 s. The function $I(c_i+)$ left-truncates the distribution at the value c_i , which is 0 for observed behaviours (i.e. the behaviour occurred at the observed time) and 600 if the behaviour did not occur within the observation period. Hence, we assumed that the right-censored observations were higher than 600 with a probability distribution estimated from the observed values and the proportion of censored measures. Birds with an unknown state (i.e. that had lost their tags or completely disappeared) were treated as missing and did not affect the survival estimates. We used weakly informative priors and conducted 100 000 iterations with a burn-in of 2000. After thinning we ended up with 10 000 simulations yielding R-hat values all below 1.02 (Brooks & Gelman, 1998; Gelman, 2014). The final model included the three behavioural measures in linear form, a unimodal effect of separation and release date.

Ethical Note

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study comply with the Swiss legislation and were in accordance with the ethical standards of the Veterinary Offices of the Cantons Lucerne, Grisons, Geneva, the Swiss Federal Office for the Environment (FOEN) and the Swiss Ornithological Institute.

RESULTS

Factors Affecting Behaviour

Emergence test

The probability of emerging within 10 min decreased with increasing baseline CORT (Table 1, Fig. 1a). There were no significant effects of strain and feeding schemes or any other predictors on

emergence probabilities. Parent ID and covey ID had significant effects on the probability of emerging (Table 1, Fig. 2a), indicating similarities between siblings and between covey mates.

In the repeated measures there was a significant quadratic effect of test date on the probability of emerging within 10 min ($x^2_1 = 19.77$, $P < 0.001$). Emergence probability decreased from test repeats 1 to 4 and increased again during repeats 5 and 6. There was no significant effect of sex on emergence probability ($x^2_1 = 0.95$, $P = 0.33$). There was a strong effect of parent ID ($x^2_1 = 13.81$, $P < 0.001$; Fig. 2a), but not individual ID. Hence, the resemblance in emergence was due to parental rather than individual factors. Also, the covey ID and test date ID were nonsignificant (all P values > 0.5 ; Fig. 2a).

Tonic immobility

The probability of recovering from tonic immobility was higher in 2010 than in 2009 and decreased throughout the season in both years (Table 1). The probability of recovering from tonic immobility within 10 min decreased significantly with increasing baseline CORT (Table 1, Fig. 1b). There was a significant random effect of covey ID but not of parent ID (Table 1, Fig. 2b).

In the repeated measures, the probability of recovering within 10 min increased linearly with test date ($HR \pm SE = 1.01 \pm 0.003$; $x^2 = 3.52$, $P = 0.001$). There were no significant effects of sex ($x^2_1 = 2.87$, $P = 0.09$), covey ID ($x^2_1 = 0.01$, $P = 0.91$), parent ID ($x^2_1 = 3.04$, $P = 0.081$) and test date ID ($x^2_1 = 2.56$, $P = 0.11$) but there was a significant individual ID effect ($x^2_1 = 10.65$, $P = 0.001$; Fig. 2b).

Separation test

Males had a lower probability of returning to conspecifics within 10 min than females (Table 1) and the return probability was around six times higher in 2010 than in 2009 (Table 1). None of the other predictors were significant (Table 1). Return probability depended on covey ID and on parent ID (Table 1, Fig. 2c).

In the repeated measures, there were strong random effects of individual ID ($x^2_1 = 18.04$, $P < 0.001$) and test date ID ($x^2_1 = 23.16$, $P < 0.001$) while the effects of covey ID ($x^2_1 = 2.56$, $P = 0.11$) and parent ID ($x^2_1 = 0.01$, $P = 0.94$) were not significant (Fig. 2c). This indicates that the resemblance in separation might be due to individual rather than parental factors. Linear and quadratic test date

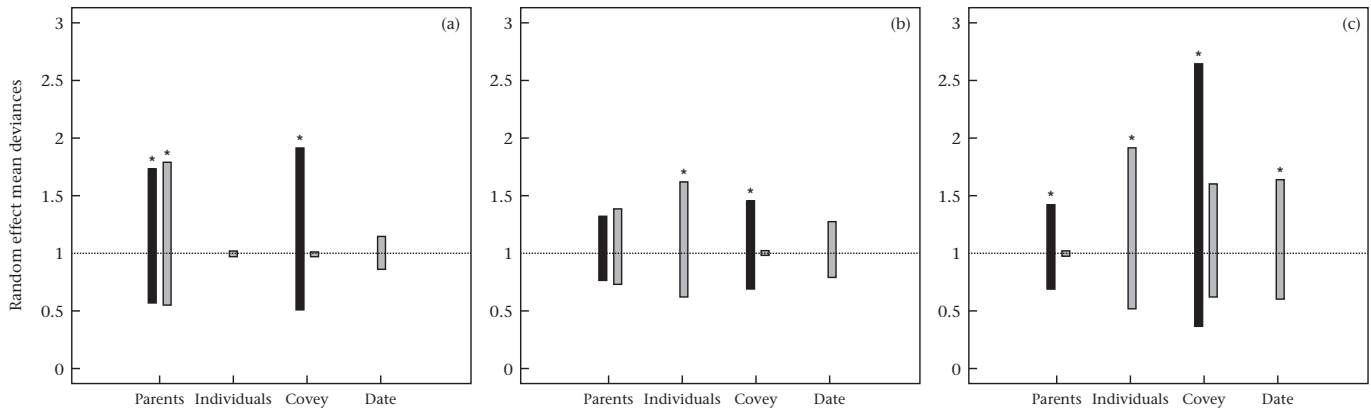


Figure 2. Variance of the random effects in the three behavioural traits in (a) emergence, (b) tonic immobility and (c) separation as obtained from the single-measure data set (black bars) and the repeated-measures data set (grey bars). The bars indicate the average variation of the event probability for each random factor around an event probability of 1 (dotted lines at $y = 1$). Longer bars indicate higher within-effect variance. Note that the random effect of individual ID cannot be estimated from the single-measure data set (black bars) and is confounded with the random effect of parent ID. * $P < 0.05$.

and sex did not significantly explain return probabilities (all P values > 0.2).

Clustering of Individuals according to Behavioural Tests

The clustering of birds according to their behaviour resulted in four clusters (Fig. 3). Cluster 1 comprised 69 (20.4%) birds and was characterized by long tonic immobility while emergence and separation times were short (Fig. 3, orange dots). Cluster 2 comprised 127 (37.6%) birds and was characterized by short test times in all three tests (Fig. 3, green dots). Cluster 3 comprised 63 (18.6%) birds. It was characterized by a long emergence time, while tonic immobility and separation times were low (Fig. 3, blue dots). Cluster 4 comprised 79 (23.4%) birds that showed long test times in all tests (Fig. 3, red dots). The four clusters differed significantly in their proportions of domesticated and wild strain birds ($\chi^2_1 = 6.41$, $P = 0.011$). Cluster 4 comprised more domesticated (54 of 187) than wild strain birds (25 of 151), while there was no difference between clusters in the proportions of prenatal and postnatal feeding schemes.

Relationship Between Survival and Behaviour

At the end of the 9-month observation period, 162 of the 177 released birds were dead (92%), two were alive and the state of 13 was unknown (Fig. A2). Survival probability was related to emergence and separation times, but not to tonic immobility (Table 2). Survival probability decreased with increasing emergence time (Table 2, Fig. 4a) and there was a quadratic effect of separation time on survival indicating that individuals with a medium separation time had a higher survival probability than those with a short or long separation time (Fig. 4b and c). Release date had a negative effect on survival (Table 2).

We predicted the cumulative survival curves for the four behavioural clusters by inserting their median behavioural test values (see Fig. 3) into the survival model of Table 2 (Fig. 5). Short emergence and separation times combined with long tonic immobility was related to the highest survival (cluster 1) whereas short emergence times were generally related to higher survival than long emergence times (Fig. 5). For birds in the field, we estimated that at the start of the breeding season (around 200 days after release), cumulative survival of the (proactive) birds with short emergence and separation times of clusters 1 and 2 was about

eight times higher than cumulative survival of (reactive and passive) birds with long emergence and/or tonic immobility and separation (Fig. 5). Survival was similar for members of clusters 1 and 2 and for members of clusters 3 and 4 (Fig. 5).

DISCUSSION

We investigated how genetic background and prenatal and postnatal environmental conditions affected the behaviours of grey partridge and how these behaviours related to each other and to survival after release into the wild. We obtained three main results. First, various pre- and postnatal factors contributed to the expression of the three behaviours, which supported the notion that they were consistent over time and provided ample variation on which selection could act. Second, based on the three measures of behaviour, birds could be assigned to four clusters which represented distinct personalities. Finally, after release into the wild, the

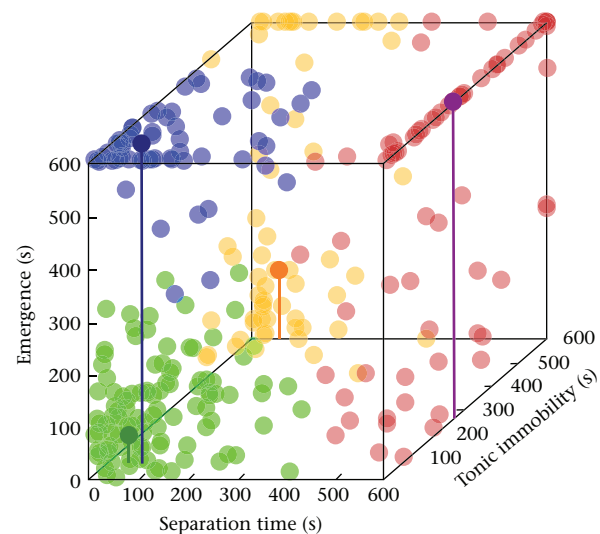


Figure 3. Three-dimensional representation of the four clusters as obtained by the cluster analysis based on 338 individuals. Coloured dots are the individual measures. Coloured dots with vertical lines to the x-y-plane show the cluster medians. Cluster 1: 69 individuals, orange dots. Cluster 2: 127 individuals, green dots. Cluster 3: 63 individuals, blue dots. Cluster 4: 79 individuals, red dots.

Table 2
Estimates of the Cox mixed-effects model of the analysis of survival

	Postrelease survival			
	HR	± 95 CI		
Fixed effects				
Emergence	1.301	1.088	to	1.561
Tonic immobility	0.921	0.755	to	1.108
Separation	0.761	0.570	to	1.010
Separation ²	1.306	0.998	to	1.727
Release date	1.431	1.054	to	1.903
Random effects				
Parents	SD = 0.004		exp(SD) =	1.004
Release date	SD = 0.003		exp(SD) =	1.003
Covey	SD = 0.008		exp(SD) =	1.008

The analysis included 177 individuals of 53 parental pairs, 15 coveys, released at 10 occasions. Parent ID, covey ID and release date were included as random effects in all analyses. All continuous explanatory variables were standardized by subtracting the respective means from each individual observation and dividing by the standard deviation. The hazard ratio (HR) indicates the change in the occurrence probability per unit change in the standardized explanatory variable. HR > 1 indicates a relatively higher and HR < 1 a relatively lower probability of mortality. CI: confidence interval.

personality types had different survival probabilities: the two clusters with rather proactive behavioural types survived significantly longer than the two types with rather passive or reactive behaviour.

Intrinsic and Extrinsic Factors Affecting Behavioural Traits

We did not find a significant effect of strain (wild/domesticated), but a genetic/parental effect was evident for the emergence test in both data sets (Fig. 2). The random effect parent ID captures the variance in emergence behaviour among families due to genetic background and prenatal parental effects (do siblings show similar test results due to their family origin?). Individuals that emerge quickly can be considered proactive and explorative (Coppens et al., 2010; Koolhaas et al., 1999; Sih et al., 2004) and exploratory behaviours in other species have been reported to be repeatable, heritable and to have a genetic basis (Edwards, Burke, & Dugdale, 2017; van Oers & Jong, 2005).

There were no clear effects of prenatal and postnatal feeding regimes on any of the three behavioural tests. Either the feeding regimes were too mild to induce stressful conditions or effects of the feeding regimes were masked by other factors. Such a factor may be covey affiliation. Covey ID quantifies variance among social groups (do members of the same covey show similar test results?). In earlier studies in grey partridge we found covey effects on various parameters from physiology to survival (Homberger et al.,

2013, 2014) which highlights the importance of the social group in this, and probably other, social species (Efferson, Lalive, Richerson, Mcelreath, & Lubell, 2008; Webster & Ward, 2011). Under natural conditions, grey partridge strongly coordinate behavioural responses within coveys to optimize, for example, antipredator responses (Tillmann, 2009). This may explain why behaviours align within coveys and are thus more similar within than between coveys. In contrast, there were no significant effects of covey ID on the behavioural tests in the repeated-measures data set. This data set allowed us to further separate variance in behaviour into the individual component (do individuals show similar test times over time?) and date component (are test results similar within test dates?). We are aware that the results of the two analyses are not fully comparable (different test individuals and test periods) and individuals probably became accustomed to the repeated test procedure which might have blurred covey effects (Bell, Hankison, & Laskowski, 2009). Nevertheless, our results indicate (Fig. 2) that grey partridge are able to develop individual behavioural strategies (in all behavioural tests), at least in the repeated-measures subgroup and/or at a later age.

Baseline CORT was positively related to both emergence and tonic immobility, supporting the concept of proactive–reactive coping styles which predicts consistent associations between behaviour and hormonal profiles (Koolhaas et al., 1999). Circulating CORT levels are partly heritable (Bézières, San-Jose, Almasi, Jenni, & Roulin, 2019; Jenkins, Vitousek, Hubbard, & Safran, 2014; Koolhaas et al., 2010) and partly depend on proximate factors such as current body condition, health state and availability of resources (Bonier & Martin, 2009; Homberger et al., 2015; Jenkins et al., 2014). Therefore, CORT levels could be part of the heritable portion of behavioural determinants and hence possess the potential for an evolutionary change in response to selection (Bézières et al., 2019; Jenkins et al., 2014; Koolhaas et al., 2010). On the other hand, it is unlikely that the highly variable levels of circulating CORT can maintain personalities over a long time (Koolhaas et al., 2010; Romero & Reed, 2008; Williams, 2008). Rather, the covariance between baseline CORT and behaviour could be mediated by underlying, slower-changing state variables such as body condition, energy reserves or body size (McElreath & Strimling, 2006; Niemelä & Dingemanse, 2018). For example, birds in poor condition could respond by increasing baseline CORT and become less active. In turn, these individuals may fail to acquire resources and deteriorate in condition which would further increase baseline CORT. State–behaviour feedbacks can lead to context-dependent behavioural and physiological reactions and may shape personalities (Creel, Dantzer, Goymann, Rubenstein, & Boonstra, 2013; Sih et al., 2015).

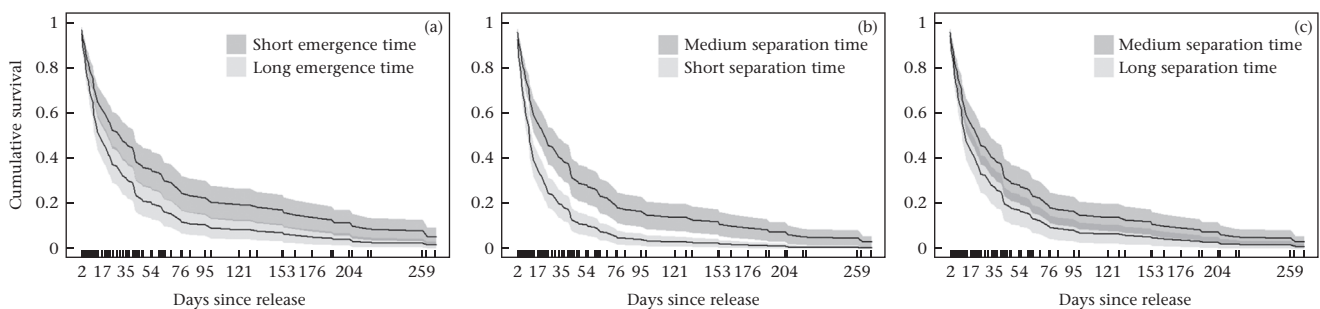


Figure 4. Predicted cumulative survival curves and 95% confidence intervals over the first 9 months after release as obtained from the survival model (Table 2). (a) Survival curves for short (50 s) and long (400 s) emergence times. (b) Survival curves for medium (300 s) and short (10 s) separation times. (c) Survival curves for medium (300 s) and long (to end of test) separation times. The prediction times were chosen to be representative of the real, raw data measures of behaviour (see Fig. A2). The ticks on the x-axis are days when death occurred.

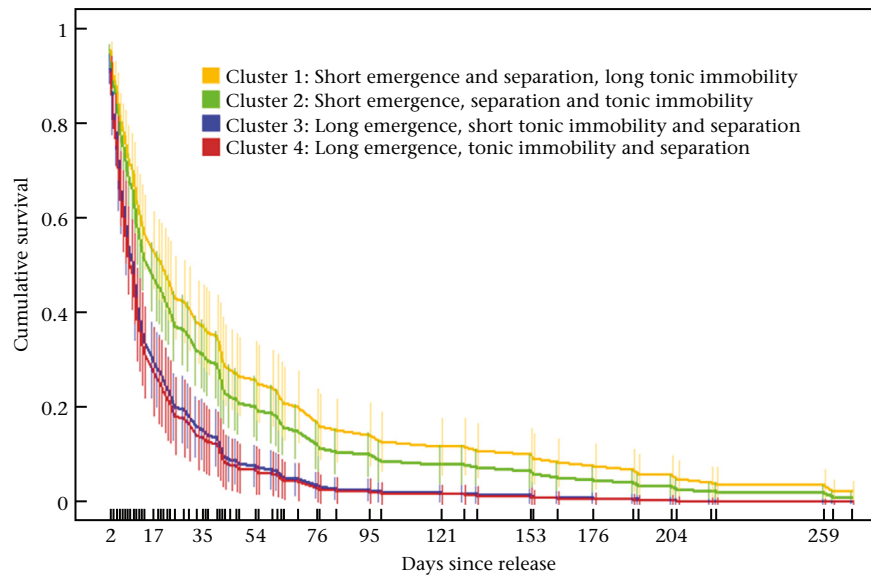


Figure 5. Predicted cumulative survival curves and 95% confidence intervals for the four behavioural clusters over the first 9 months after release as predicted from the survival model (Table 2). The ticks on the x-axis are days when death occurred.

We found no effect of stress response CORT on behaviour tests which was surprising since wild strain birds showed higher CORT stress responses than domesticated strain birds (Homberger et al., 2015). While associations between behaviour and CORT stress response have been found elsewhere, it has also become clear that CORT stress responses can differ markedly between species and between individuals (Cockrem, 2013). As described here, there are various factors associated with our measurements of behaviour and our test setting in captivity might have induced variation that might have concealed effects of stress response CORT (Bell et al., 2009).

In summary, behavioural traits, as used here, were determined by a mixture of genetic/parental effects (emergence), the social environment (all three tests), the immediate nonsocial environment (test date) and possibly also acquired individual strategies (tonic immobility and separation). Hence, the behaviours did not arise from single pivotal mediating factors as expected under the 'constraint hypothesis', but were governed by multiple independent intrinsic and extrinsic factors ('adaptive hypothesis'; Ketterson & Nolan, 1999; Wilson, 1998).

Behavioural Types and Their Survival in the Wild

There were no clear linear relationships between the three behavioural tests, which indicates that they measured different and largely unrelated aspects of behaviour. The clustering technique revealed four clusters with distinguishable personalities and different postrelease survival. Interestingly, we found that in an isolated context short emergence times supported survival after release whereas fast emergence in a social context was related to low survival.

To better understand this result it might be appropriate to consider the motivations, decisions and actions involved at the individual level (Wilson, 1998). First, an individual has to be able and willing to be active in any given context (activity versus passivity). Second, if an individual is able and willing to be active, the underlying motivation might determine the behavioural

response. Emerging fast in an isolated context can be considered a proactive, explorative behaviour. However, when facing conspecifics, quickly returning to the covey mates could represent a reactive response, that is, finding shelter among the group mates as quickly as possible.

When applying this reasoning to our personality types, clusters 1 and 2 were both characterized by proactive individuals that quickly emerged into an unknown environment. Also, they reacted to the presence of conspecifics by actively seeking social reinstatement. These proactive behavioural types survived longest after release into the wild. Proactive clusters 1 and 2 differed in tonic immobility which can be considered an antipredator behaviour (Miyatake et al., 2009). Birds of cluster 1 had short emergence and separation times but long tonic immobility implying more appropriate antipredator responses compared to birds of cluster 2 with short test times in all three tests. Accordingly, survival of cluster 1 birds was marginally higher than that of birds of cluster 2. Cluster 3 birds were characterized by short tonic immobility and separation times but long emergence times. Rather than proactively exploring an unknown environment, birds of cluster 3 simply reacted to the presence of conspecifics. They tended to remain passive in an isolated context but sought shelter among the covey mates in a social context. Birds of cluster 4 remained passive during emergence and did not react to the presence of conspecifics. They seemed overwhelmed by the test setting and unable to act proactively. Accordingly, birds of clusters 3 and 4 showed lower survival than those of clusters 1 and 2, and survival was lowest for the least responsive birds of cluster 4. Interestingly, we found a high proportion of domesticated strain birds in the passive cluster 4 which suggests that despite adaptation to captivity over many generations, birds of the domesticated strain were less able to cope with the unusual experimental settings and challenges of the post-release environment (McDougall, Réale, Sol, & Reader, 2006).

Note that survival rates found in our study were generally low but comparable to those of other reintroductions (Buner, Browne, & Aebischer, 2010; Meriggi, Brangi, Cuccus, & Stella, 2002). This shows that despite effective habitat improvements at our release

sites, it is very difficult to re-establish viable populations from captive-reared birds (Buner, Jenny, Zbinden, & Naef-Daenzer, 2005; Lanz, Michler, & Duplain, 2012). A main problem of our and many other reintroductions was a high predation rate (Homberger et al., 2014; Moseby et al., 2011).

Negative associations have been postulated and repeatedly described between proactive, bold behaviour, survival and longevity (Dammhahn et al., 2018; Smith & Blumstein, 2007). For example, in a release project of swift foxes, *Vulpes velox*, individuals that were characterized as more active and bolder in captivity moved, on average, further from the release site and had lower survival than less active, more fearful individuals. These negative associations have recently been put into perspective (Moirón, Laskowski, Niemelä, & Gurevitch, 2019). Proactive behaviour could be especially relevant in the context of planned introductions or unintended animal invasions (Chapple, Simmonds, & Wong, 2012) and could facilitate the colonization of new habitats (Bremner-Harrison et al., 2004; González-Bernal, Brown, & Shine, 2014).

Under fluctuating environments, or changing needs of different life cycle stages, the benefits and drawbacks of a particular personality may change or even be reversed (Sih et al., 2004). In grey partridge we found anecdotal evidence for this. During courtship, females prefer males that show high vigilance behaviour (Dahlgren, 1990). In a small sample, we found that a long emergence time was positively correlated with male vigilance during courtship (Reding & Homberger, 2010; eight males tested in a mate choice experiment). Thus, emergence time was not only negatively related to survival but also positively related to vigilance behaviour during courtship which would result in a conflict between sexual and natural selection. Such conflicts can have far-reaching consequences for ecology, evolution and conservation of species (Dochtermann & Dingemanse, 2013; McDougall et al., 2006). For example, if only proactive grey partridge males survived the early reintroduction phase, females would have to put up with non-preferred proactive males (probably imprudent fathers) which would lower their reproduction success. It will be important to further investigate how selection at different levels affects animal personalities and how variance in behaviour can persist in fragmented populations (Adriaenssens & Johnsson, 2013).

Conclusions

We draw two main conclusions from this study. First, the three behavioural traits appear to be relatively flexible (responsive to multiple factors) and cluster into a proactive–reactive spectrum. Genetic/parental effects as well as the social context and individual experience appear to be important modulators of behaviour. Individuals can acquire their own behavioural strategies, that is, they can adjust behaviour according to context and could ultimately exhibit adaptive individual differences in behaviour.

Second, proactive behaviour was related to higher survival in the wild, an association presumably pronounced in the context of introduction into an unknown environment. While proactive behaviour supported survival, it might detrimentally affect performance in later life history stages such as breeding. It would be interesting to see whether behaviour and behavioural types remain responsive to intrinsic and extrinsic factors throughout life which will require longitudinal studies in wild populations under changing environmental conditions.

Acknowledgments

We thank David Butler, Christian Dextl, Nina Keller, Imelda Schmid and many field assistants for their support when rearing, transporting, releasing and radiotracking partridge. Gilberto Pasi-nelli, Roman Furrer, Ruedi Nager, Josh Firth and an anonymous referee provided valuable comments on the manuscript. This work was supported by the Swiss National Science Foundation, Switzerland (grant no 31003A_127057 to LJ and SJ-E).

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Appendix

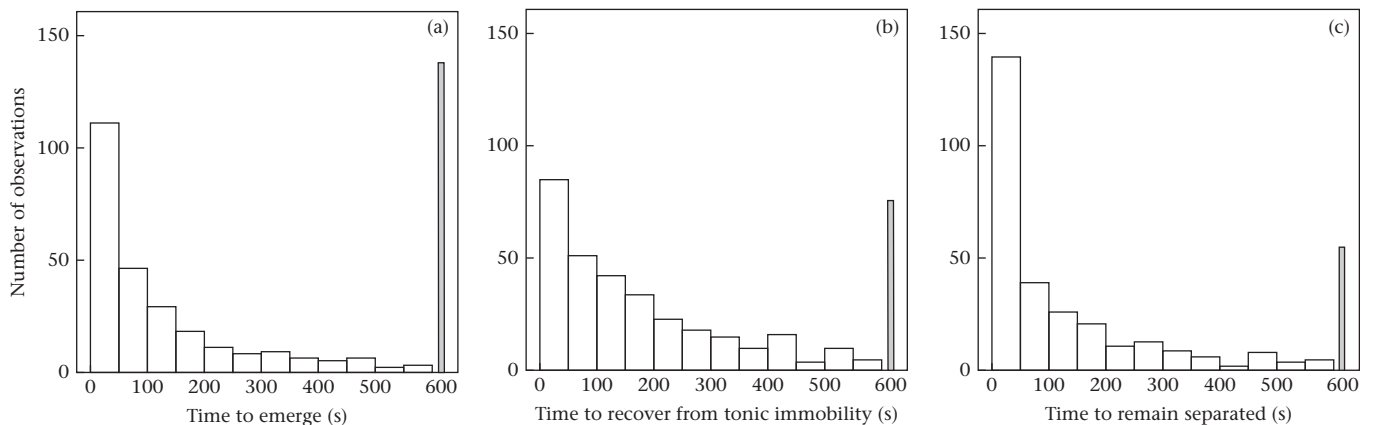


Figure A1. Frequency distributions of the times (a) to emerge based on 391 individuals, (b) to recover from tonic immobility based on 389 individuals and (c) to remain separated from conspecifics based on 341 individuals. The grey bars at time 600 give the number of individuals that did not show the respective behaviour within 10 min.

Table A1 Full model estimates of the Cox mixed-effects models for the analysis of the three behavioural test measures as obtained from the single-measure data set

	Emergence				Tonic immobility				Separation						
	HR	± SE	z	P	HR	± SE	z	P	HR	± SE	z	P			
Fixed effects															
Strain (wild)	1.148	0.775	to 1.522	0.37	0.710	1.057	0.772	to 1.342	0.19	0.850	1.008	0.665	to 1.352	0.02	0.980
Prenatal food supply (unpredictable)	1.168	0.814	to 1.521	0.44	0.660	1.075	0.795	to 1.355	0.26	0.800	0.865	0.522	to 1.208	-0.42	0.670
Postnatal food supply (unpredictable)	0.783	0.526	to 1.040	-0.95	0.340	1.184	0.959	to 1.408	0.75	0.450	0.961	0.704	to 1.218	-0.15	0.880
Corticosterone baseline	0.979	0.969	to 0.989	-2.18	0.029	0.985	0.976	to 0.994	-1.73	0.084	1.007	0.998	to 1.016	0.75	0.450
Corticosterone stress response ¹	1.002	0.999	to 1.006	0.75	0.450	0.999	0.996	to 1.002	-0.34	0.730	1.004	1.001	to 1.008	1.25	0.210
Sex (male)	1.115	0.955	to 1.274	0.68	0.500	1.146	1.005	to 1.287	0.97	0.330	0.627	0.466	to 0.789	-2.89	0.004
Body mass	1.001	0.998	to 1.005	0.42	0.680	0.999	0.996	to 1.002	-0.41	0.680	1.006	1.002	to 1.009	1.61	0.110
Year (2010)	1.119	0.721	to 1.518	0.28	0.780	2.142	1.858	to 2.425	2.69	0.007	5.158	4.561	to 5.754	2.75	0.006
Test date	1.443	1.190	to 1.696	1.45	0.150	0.894	0.715	to 1.074	-0.62	0.530	1.007	0.592	to 1.421	0.02	0.990
Test date squared	0.999	0.999	to 1.000	-1.43	0.150	1.000	1.000	to 1.001	0.76	0.450	1.000	0.999	to 1.001	0.05	0.960
Strain*prenatal treatment	0.658	0.138	to 1.179	-0.80	0.420	0.856	0.452	to 1.260	-0.39	0.700	0.892	0.413	to 1.371	-0.24	0.810
Strain*postnatal treatment	1.166	0.727	to 1.604	0.35	0.730	0.852	0.476	to 1.228	-0.43	0.670	1.540	1.105	to 1.975	0.99	0.320
Prenatal*postnatal treatment	1.166	0.740	to 1.593	0.36	0.720	0.836	0.474	to 1.199	-0.49	0.620	1.338	0.915	to 1.762	0.69	0.490
Strain*prenatal*postnatal treatment	1.140	0.500	to 1.780	0.21	0.840	0.738	0.182	to 1.295	-0.54	0.590	0.71302	0.099	to 1.327	-0.55	0.580
Random effects															
Parents	SD = 0.51	exp(SD) = 1.67	$\chi^2 = 22.30$	$P < 0.001$	SD = 0.24	exp(SD) = 1.27	$\chi^2 = 1.25$	$P = 0.262$	SD = 0.44	exp(SD) = 1.55	$\chi^2 = 9.34$	$P = 0.002$			
Covey	SD = 0.59	exp(SD) = 1.80	$\chi^2 = 13.11$	$P < 0.001$	SD = 0.39	exp(SD) = 0.44	$\chi^2 = 19.13$	$P < 0.001$	SD = 1.04	exp(SD) = 2.82	$\chi^2 = 76.08$	$P < 0.001$			

The models of the emergence and tonic immobility tests included 321 individuals of 62 parental pairs and 22 coveys. The separation test included 338 individuals of 22 coveys and 66 parental pairs. Parent ID and covey ID were included as random effects in all analyses. The hazard ratio (HR) for continuous variables indicates the change of the occurrence probability per unit change in the explanatory variable. HR > 1 indicates a relatively higher and HR < 1 a relatively lower probability of occurrence of the behaviour.

¹ Coefficients and statistics for corticosterone stress response when included as a predictor instead of baseline corticosterone.

