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ORIGINAL ARTICLE

Unravelling the relationships between life history, behaviour and condition under the pace-of-life syndromes hypothesis using long-term data from a wild bird

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Abstract

The hypothesis of pace-of-life syndromes (POLS) predicts relationships between traits including life history traits and risk-taking behaviour that can be mediated by the trade-off between current and future reproductive value. However, alternative causal mechanisms may also generate covariance among these traits without trade-offs. We investigated the relationships between survival to the next year, current reproductive investment and risk-taking behaviour (flight initiation distance) in male collared flycatchers, *Ficedula albicollis*, using long-term data. We used structural equation modelling (SEM) to uncover whether the associations among traits are mediated by a common latent factor that determines how individuals balance the trade-off between current and future reproductive value. As trade-offs could be concealed when there are differences in resource acquisition between individuals, we also included potential causes of these differences, body mass and body size, in the analysis. We found that risk-taking behaviour was positively related to reproductive investment and negatively to survival to the next year as could be predicted if investment into a risky behaviour is traded against future prospects. However, the most supported SEM model also suggested that survival to the next year was positively related to current reproductive investment, contrary to predictions of a hypothesis based on trade-off. These results remained qualitatively similar when controlling for body condition. In conclusion, we only could derive partial support for the POLS hypothesis. We suggest that aspects of individual quality, and not only trade-offs, should also be considered when interpreting the relationships between life history and behavioural traits.

Significance statement

We investigated the association between two life history components (survival to the next year and current reproductive effort) and risk-taking behaviour, relying on long-term records from a passerine bird, to investigate the predictions of the pace-of-life

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syndrome (POLS) hypothesis. Using structural equation modelling, we found support for a causal model that implies that risk-taking negatively affects survival to the next year and that survival to the next year and current reproductive effort are strongly and positively associated. Controlling for the effect of body condition did not fundamentally change these relationships. We could not find conclusive evidence for the investigated traits being mediated by a common underlying factor, as generally predicted by the POLS hypothesis. However, the sign of the relationship between risk-taking behaviour and survival to the next year was as predicted by the POLS hypothesis.

Keywords Behavioural syndrome · Fitness · Model selection · FID · Passerine · Personality

Introduction

The hypothesis of pace-of-life syndromes (POLS) posits that life history traits varying along a slow-fast continuum correlate also with specific physiological and behavioural traits (generally risk-taking and active behaviours) at the interspecific level, creating a syndrome between these traits and determining how species or populations cope with different environments in a multifaceted way (Ricklefs and Wikelski 2002; Biro and Stamps 2008; Réale et al. 2010). These links can also exist at the within-species level, since individuals also maintain consistent differences in their behaviour and life history (Wolf et al. 2007; Réale et al. 2009, 2010). The fundaments of the POLS hypothesis are well established (Réale et al. 2010 and other papers in this POLS Topical Collection), but, due to the lack of theoretical models and the equivocal empirical results, several questions remain to be answered, especially at the within-species level (Mathot and Frankenhuis 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes). These questions include the generality of the hypothesis, the list of traits considered as components of POLS, the underlying causal mechanisms, the strength of the predicted relationships among different traits and the effect of potential ecological factors that can decouple the traits of POLS within a population (Dingemanse et al. 2004; Niemelä et al. 2013; Závorka et al. 2016; Mathot and Frankenhuis 2018, topical collection on Pace-of-life syndromes; Montiglio et al. 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes).

Concerning the underlying mechanism, the trade-off between present and future reproductive value is often regarded as the most important mechanism of POLS, and the life history traits involved in this trade-off are connected to behaviours that usually influence assets but also imply mortality cost (McNamara and Houston 1989; Clark 1994; Wolf et al. 2007; Engqvist et al. 2015; Fig. 1a). Risk-taking behaviours that are manifested in situations involving immediate risk, i.e. those that expose the individual to predation threat, diseases or elevated physiological costs, may fulfil this criterion (Réale et al. 2007). The asset protection hypothesis, for example, is based on the trade-off between present and future reproductive value and it states that if an animal's expectations of reproductive success (or assets) are low for the future, the level of its risk-taking behaviour will be elevated (Clark 1993, 1994; Wolf et al. 2007). Thus, this trade-off can be regarded as a latent underlying factor that delineates the fast-slow continuum and that causes the correlation structure between the POLS traits (Dingemanse et al. 2010).

Although the POLS hypothesis emphasizes that the trade-off between current and future reproduction underlies the relationship between different traits, alternative causal mechanisms may also lead to correlations among phenotypic traits (see also Mathot and Frankenhuis 2018, topical collection on Pace-of-life syndromes; Royauté et al. 2018, topical collection on Pace-of-life syndromes). For example, growth-mortality trade-off may also trigger associations between life history and morphological and certain behavioural traits (Stamps et al. 1998; Mangel and Stamps 2001; Stamps 2007). Other possible mechanisms not involving trade-offs are e.g. correlational selection and gene pleiotropy (Sinervo and Svensson 2002; Sih et al. 2004). Gene pleiotropy, for example affecting through corticosterone, may represent a common factor influencing multiple traits that creates syndromes similarly to life history trade-offs (Bell 2005; Garamszegi et al. 2012).

Regarding the confounding effect of ecological factors, the local environmental conditions or certain individual traits may alter or even conceal the POLS structure in the population (Montiglio et al. 2018, topical collection on Pace-of-life syndromes). For example, in models assuming a trade-off between present and future reproductive value and a relationship with risk-taking behaviours, the outcome of the strategies may depend on the actual costs associated with risky behaviour and the variation of resource acquisition among individuals (van Noordwijk and de Jong 1986; Engqvist et al. 2015). In terms of life history, individuals with more acquired resource, which could result in good body condition or of high general quality (van Noordwijk and de Jong 1986; Peig and Green 2009), may also have more offspring along with increased longevity, as between-individual variation in the resource acquisition may mask the trade-off between current and future reproductive value (van Noordwijk and de Jong 1986). Regarding the risk-taking behaviour, individuals with higher energy reserves should continue their normal activity further under predatory threat, taking more risk behaviourally and saving the cost of fleeing (Ydenberg and Dill 1986; Martín et al. 2006; Jablonszky et al. 2017; Fig. 1b), as stated also by the state-dependent safety hypothesis (Luttbeg and Sih 2010).

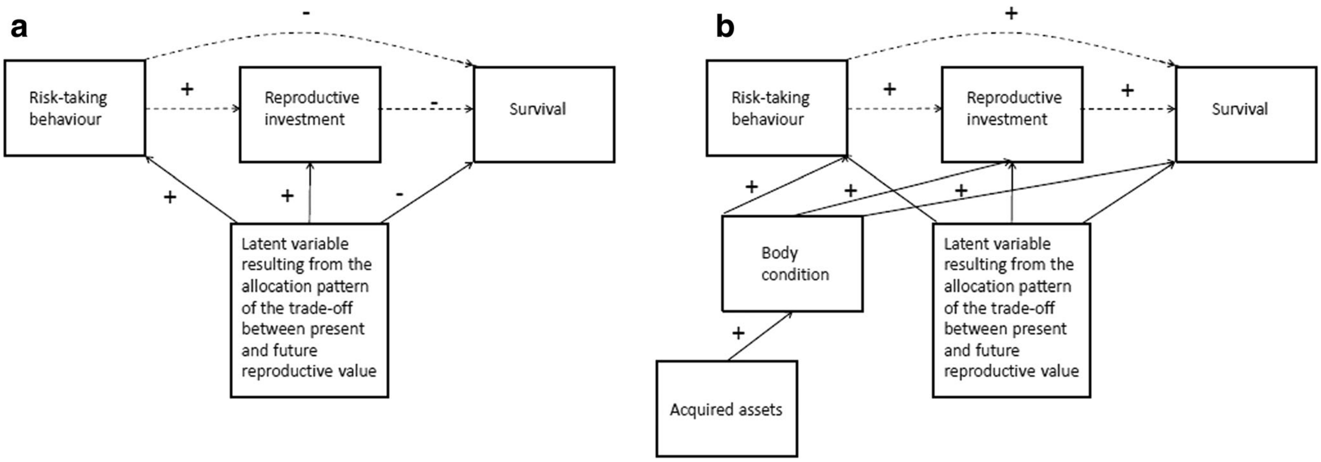

Fig. 1 Conceptual figures of two hypotheses described in the "Introduction" section. The hypothetical relationships between the focal variables are displayed **a** based on the POLS hypothesis implying the trade-off between present and future reproduction as underlying mechanism and **b** based on the mechanism involving differences in assets. Solid lines represent putative causal mechanisms, while dashed lines represent indirect among individual relationships that could be observed at the phenotypic level

According to this latter hypothesis under intermediate natural conditions (predation risk, resource availability), individuals with more initial resources will be bolder in front of predators through positive feedback mechanism between state and behaviour (Luttbeg and Sih 2010).

A common measure of risk-taking behaviour in many animal taxa is flight initiation distance (FID), i.e. the distance at which the individual flees when a potential predator approaches (Blumstein 2006). Therefore, shorter distances reflect higher risk-taking. FID is repeatable within individuals (Carrete and Tella 2010; Møller 2014) and appears to be heritable (Møller 2014). Its repeatability is higher within than between years, suggesting that FID may be connected to life history traits within a single breeding season (Garamszegi et al. 2015). FID is linked to survival, probably because it is related to predation risk (D'Anna et al. 2012; Møller 2014). Moreover, previous studies found FID to differ between urban or rural habitats according to the different types and abundance of predators (Uchida et al. 2016; Sol et al. 2018, topical collection on Pace-of-life syndromes). Furthermore, FID could be related to reproductive success through mating display and pairing speed or through nest site selection (Garamszegi et al. 2008; Seltmann et al. 2014; Zhao et al. 2016). Finally, FID is also related to life history at the across-species level (Blumstein 2006; Møller and Garamszegi 2012).

The aims of our empirical study were to investigate whether a correlation between risk-taking behaviour, survival and reproductive investment, as predicted by POLS, exists among individuals in a wild population of collared flycatcher (*Ficedula albicollis*) and, if so, whether the relationship among the traits involved is mediated by a trade-off between current and future reproductive value (Gustafsson and Sutherland 1988). We used data on life history (survival to the next year, current reproductive investment), risk-taking behaviour (FID) and body condition (body mass relative to body size) from our long-term records of 9 years. The POLS hypothesis assumes that the relationships among traits may be mediated by life history trade-offs; thus, we predicted that risk-taker individuals would have lower survival probability to the next year and lay larger clutches representing a faster lifestyle. As trade-offs can be concealed by the effect of size-related differences in resource acquisition on the elements of the trade-off and more likely detected when individuals are under constraints (i.e. when they are in poor condition or have to make extreme investments) (Marden et al. 2003; Briga et al. 2017), we also investigated if the POLS structure is more emphasized when controlling for body condition. To test these predictions, we adopted a statistical framework based on the structural equation modelling (SEM) approach that can handle multiple response and explanatory variables simultaneously and also latent variables representing the common mechanism potentially mediating the relationship among the investigated phenotypic traits (Dingemanse et al. 2010; Dochtermann and Jenkins 2011).

Methods

Study site and study species

Our study area is a mainly oak-dominated, contiguous woodland in the Pilis-Visegrádi Mountains, Hungary (47° 43′ N, 19° 01′ E), which is the part of the Duna-Ipoly National Park. The first study plots were established in the early 1980s (Török and Tóth 1988), and they currently contain around 800 nest boxes, in which our model organism, the collared flycatcher, commonly breeds. The study area now consists of multiple plots close to each other. Reproductive investment and the survival have been regularly and intensively monitored since the establishment of our research area via standard capturing and ringing protocols as well as regular nest box checks during the breeding season (Török and Tóth 1988).

The collared flycatcher is a small, hole-nesting, long-distance migratory species that arrives at our breeding site from Africa in the middle of April. It is a relatively short-lived bird with a maximum lifespan of 8–9 years, but only around 10% of the population live more than 5 years (Pärt et al. 1992). Males arrive earlier than females and compete for nest boxes to attract females by conspicuous courtship behaviour. After courtship and mating, females lay and incubate 4–8 (mainly 6–7) eggs. After hatching, both parents feed and take care of the chicks that start to fledge from 14 days of age onward (Cramp and Perrins 1994).

Field work

For this study, we used field data on the life history traits, morphology and behaviour of male collared flycatchers from 2007 to 2016 (except 2008 due to small sample size, $N = 3$, see more details about sample sizes in the Supplementary Table S2). We assayed the risk-taking behaviour of males in a standard way by measuring FID during the courtship period (Garamszegi et al. 2008). We could gather these data for males only, because during courtship their behaviour can be assessed around the occupied nest box, while females cannot be localized reliably in this period.

The procedure for estimating FID was as follows. First, we located displaying unmated males on their territories just after their arrival from the wintering sites. We assumed that the first day of observation at the breeding sites reflects arrival date, because we monitored the study area on a daily basis for newly arrived males. Then, we triggered territorial aggression by placing a decoy male flycatcher in a small cage representing an intruder for the focal male on its occupied territory (Garamszegi et al. 2006). In this way, we made sure that all of the tested males were responding to the same stimulus and were engaged in the same background activity before measuring FID. When we observed the focal male on the decoy male's cage showing clear intention to fight or on the nest box displaying typical territorial behaviour, the observer started to walk from a distance of about 30 m towards the focal male at normal walking speed. We continued this process until the male noticed the approaching observer and flew away from the reference point (cage or nest box). At this point, the observer halted the approach and waited standstill. If the focal male returned to the reference point to continue the original activity within 1 min, the observer started to approach the male again. This was done in order to measure the real risk-taking behaviour instead of the ability to notice the observer. This process was repeated until the focal male did not return within a minute. The risk-taking behaviour of the male was then measured by the number of steps (approximately 1 m) between the decoy male's cage and the last position of the observer at which the focal male did not continue its territorial behaviour. Accordingly, FID is an inverse measure of risk-taking, as risk-taker individuals allow a potential predator to approach them at a closer distance than risk-averse individuals. The FID measurements were carried out by six trained experimenters. Between-observer effects were not accounted for in the statistical models to avoid too complex models and because a previous study indicated that these effects are negligible (Jablonszky et al. 2017). When carrying out the behavioural assays, information on life history and morphology of the focal individual was unknown for the experimenter; thus, criteria for blind experimentation were met. Given the sequence of our field protocols, this principle was also guaranteed for the other phenotypic traits (see below).

We are aware that when studying behaviour, it is advised to separate between- and within-individual effects (Dingemanse and Dochtermann 2013). Information on FID from the same individual was available in our data for more than one year for 19 birds (see more details in the Supplementary Table S1). However, when we performed our analyses based on our whole dataset including repeated measurements for these 19 males and by including bird identity as a random factor, we derived unstable models (see more details below, multivariate potential scale reduction factor 2.73). Therefore, we continued our analysis based on a dataset that included the first entry for each individual and did not consider random effects.

Morphological measurements

After the behavioural measurement, we captured the assayed males in their nest boxes by conventional spring traps and measured morphological variables and ringed them. We could not capture 22.22% of the birds, but it could not bias our results due to potential repeated testing of FID on some individuals, because we included only captured birds in the analysis. However, it is possible that our sample is biased, and including the whole population (also the shyest uncaptured birds) in the analysis could result in stronger correlations, as trappability is positively correlating with FID in our population ($r = 0.67$, Garamszegi et al. 2009). Further bias may emerge from the fact that an uncaptured bird measured for the second time may habituate to the test and produce lower FID estimates. However, the repeatability of FID in our population (Garamszegi et al. 2015) and the fact that experience with the procedure of FID did not affect the actual measurement of FID in our previous study (Jablonszky et al. 2017) indicate that the influence of this bias is low. Nevertheless, we took into consideration these biases when interpreting the results. We measured body mass using Pesola spring balance (with a precision of 0.1 g), and the length of tarsus reflecting body size using calliper (with a precision of 0.1 mm). We also determined the age of each male based on their plumage, given that 1-year-old birds bear brown remiges and smaller white patches, while remiges of older males are black and their patches are larger (Mullarney et al. 1999). After measurements, males were marked with individually numbered rings for long-term identification; thus, the reproductive success of all birds was monitored throughout the breeding season based on systematic nest box checks and high effort to capture the parents during nestling care.

Life history traits

The number of ringed chicks (8–10 days old) represented the current reproductive effort of the focal male. Though it underestimated reproductive effort, we used this measurement, because it is highly correlated with the number of fledglings ($r_{\mathrm{sp}} = 0.88$, $N = 196$, $p < 0.001$), and we have greater sample size for this measurement than for the latter due to predation and other accidental causes of nest failure that made uncertain the enumeration of fledglings. Nevertheless, we present results with the number of fledglings in the Supplementary Tables S8–S10. Survival to the next year was estimated based on whether we recaptured the focal bird in the subsequent breeding season (i.e. we considered individuals that were not observed breeding in the next year as dead). This approach potentially underestimates true survival, due to failure of capture, but the incidence of a previously ringed individual not being observed breeding in one year but being recaptured in the next year is very rare (< 5%, JT unpublished data). Furthermore, survival analyses in our study population that can account for differences in recapture probabilities revealed that conclusions based on survival estimates from capture-mark-recapture models are very similar to those that are based on recapture probability (Garamszegi et al. 2004a). Another confounding effect is permanent emigration (Perlut and Strong 2016), which we could not measure. However, we can assume that the effect of emigration is moderate at the best, because the collared flycatcher is a highly philopatric species (Pärt 1990; Garamszegi et al. 2004a). Reproductive costs (such as decrease in juvenile survival, parent and offspring fecundity, identified by clutch size manipulation experiments) have been detected for this species (Gustafsson and Sutherland 1988). However, longevity is positively linked to lifetime reproductive success and mean recruits per year in our population (Herényi et al. 2012).

Statistical analysis

We assumed that among the investigated traits, FID is consistent and also, the other two (survival, reproductive investment) are individual-specific at least within a breeding season. These assumptions were based on the known within-year repeatability of FID (Garamszegi et al. 2015) and the fact that typically only one breeding attempt is made in a year; thus, a single year-specific reproductive investment and survival value are applicable to each individual.

To estimate the correlation matrix of traits necessary for the SEM models, we used the point estimates of correlations from a Markov chain Monte Carlo Bayesian generalized linear model (MCMCglmm; Dingemanse and Dochtermann 2013; Mutzel et al. 2013; Brommer et al. 2014), which allows multiple response variables to follow different distributions, such as Gaussian or binomial (Hadfield 2010). For the first set of analyses, we estimated the correlation between survival to the next year, the number of ringed chicks and FID and entered them as tri-variate response variable into the model. We included age (1 year old or older), date, year and plot as fixed effects to control for the seasonal, annual and spatial variation (Brommer et al. 2014). Date of observation was standardised across years by re-coding it relatively to the encounter with the first male displaying the typical territorial behaviour in the given year. Although we only wanted to derive a correlation matrix of the response variables from these models, the control variables were necessary because they had been found to affect our response variables. FID, reproductive investment and survival can vary with age (Brommer et al. 2007; Réale et al. 2009; Sanz-Aguilar et al. 2015; Jablonszky et al. 2017). The arrival date at the breeding site, reflecting by the date of the behavioural test, is very important in this species, because as long-distance migratory birds, they face a considerable time constraint on reproduction (Wiggins et al. 1994). In addition, date can reflect territory quality, as early arriving males have higher chance to occupy good territories than late arriving conspecifics. Furthermore, year- and plot-specific environmental quality could affect reproductive success (Török and Tóth 1988; Garamszegi et al. 2004b; Török et al. 2004) and also could alter the relationship between risk-taking behaviour and reproductive success (Patrick and Weimerskirch 2014). We used only records with no missing data, to be able to run the below two models on the same dataset ($N = 234$). The normality of the response variables, except survival to the next year, was checked and consequently, FID was square root transformed. This transformation was also biologically justified because we infer that the absolute differences between two FID values may be less meaningful on their original scale (Houle et al. 2011). All of the response variables, except survival to the next year, were z-transformed. We defined priors necessary for the Bayesian modelling with the inverse Wishart distribution for the residual variance structure, with a diagonal matrix containing the raw variances of the variables, except survival to the next year, for which it was fixed to 1 because it was a binomial variable (see additional information about results with other priors in the Supplementary Text S1). The degree of freedom parameter for the prior was equal to the number of the response variables (Hadfield 2010). The models ran for 510,000 iterations, with 10,000 samples discarded at the beginning and with a thinning interval of 500. The trace and distribution of all variables were checked visually, as well as autocorrelation between iterations. Additionally, mixing and convergence were checked with Gelman-Rubin statistics (Gelman and Rubin 1992).

We investigated the relationships among survival to the next year, the number of ringed chicks and FID as predicted by the POLS hypothesis using SEM. We constructed SEM models reflecting different causal scenarios that we challenged with our data in two steps. First, we described the potential causal relationships among the focal traits via eight different SEM models (Fig. 2). The null model assumed no relationship between the three variables, while we constructed the other models abiding the following three guidelines. (1) We followed the general principles for building SEM models (Ullman 2006), e.g. one latent variable should have at least three indicator variables. (2) The order of causality reflected the order of manifestation or measurement of our variables (e.g. current reproductive investment should always precede survival to the next year). (3) The considered causal links could be interpreted biologically. We created a model that contained a latent variable according to the hypothesis of POLS assuming common syndrome structure. We also constructed a set of models that did not include a latent variable representing alternative causal mechanisms, i.e. assuming direct link between the focal variables. Based on these criteria, in our candidate model set, we covered all possible combinations of causal links with biological meaning among the investigated and the latent variables (the biological interpretations of these models are presented in the Supplementary Text S2).

For the second step of analyses, in the MCMCglmm models, from which the correlation matrix necessary for the SEM was derived, we entered also tarsus length and body mass as control variables to account for the effect of body size and body condition, which could result from the amount of resources the individual acquired prior the behavioural assays and making reproductive decisions. Body mass moderately correlates with body size (i.e. tarsus length, $r = 0.29$, $N = 234$, $p < 0.001$), but we intended to control for the combined effect of these two variables (and not to estimate their partial effect), so collinearity did not pose a problem in this sense. Body condition could reflect the energy reserves of the individual and is usually estimated as residuals from mass-tarsus

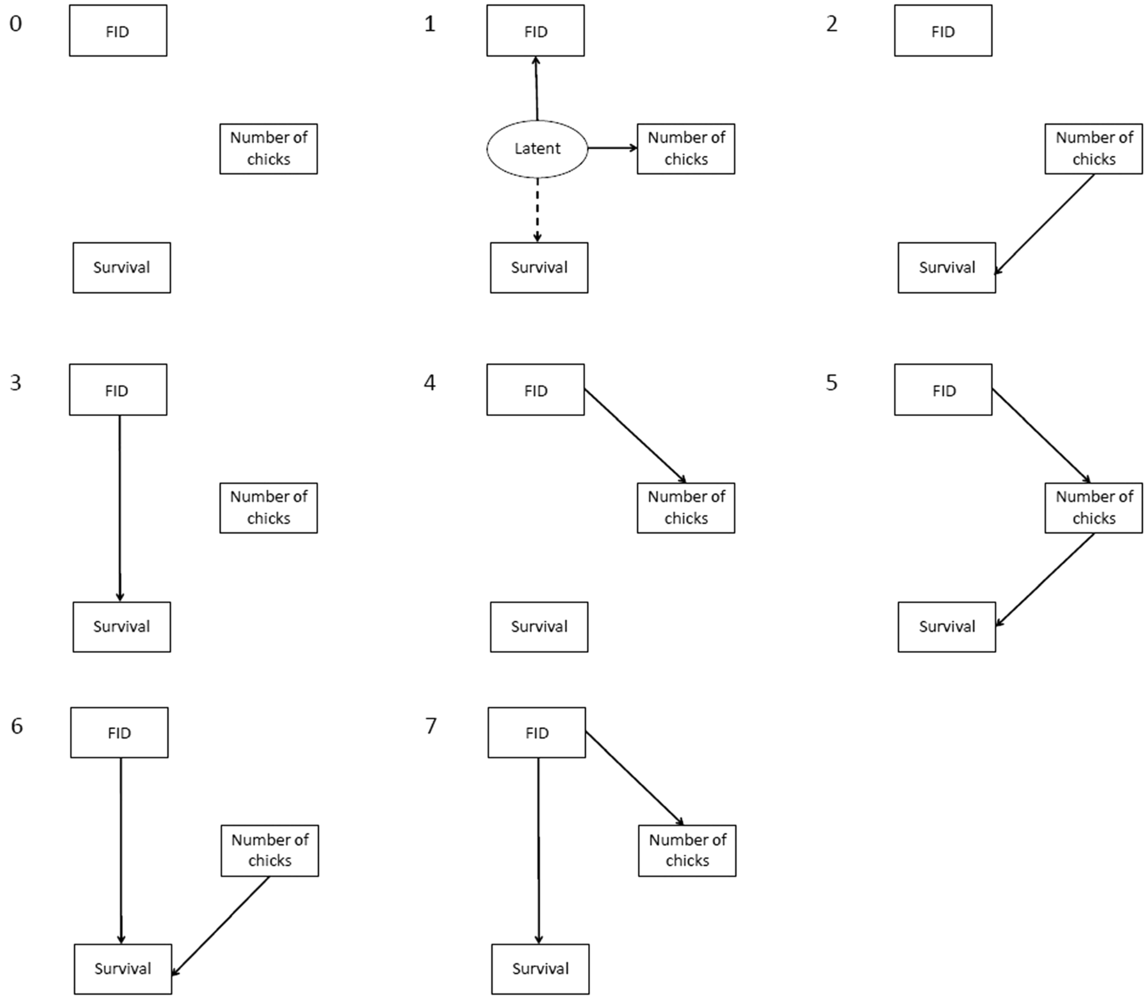

Fig. 2 The eight structural equation models (SEM) depicting the possible relationships between survival to the next year, the number of ringed chicks and flight initiation distance (FID) of the male collared flycatchers. Squares represent measured variables, while the circle represents the latent variable. Solid arrows depict direct relationship between the variables. Dashed line indicate fixed relationship

regression in our study species, i.e. body mass relative to body size (Schluter and Gustafsson 1993; Sheldon et al. 1997; Rosivall et al. 2009). Birds developing in poor feeding conditions in nestling ages are lighter and have smaller tarsi when adults, which suggests that assets acquired by the individual can influence both body mass and body size (Merilä 1997; Krause et al. 2017). We further argue that body size and body mass are associated with assets because traits like body condition or tarsus length have been found to influence both components of fitness in the collared flycatcher (Alatalo and Lundberg 1986; Lindén et al. 1992; Schluter and Gustafsson 1993; Andersson and Gustafsson 1995; Szöllősi et al. 2009), although not in every study (Herényi et al. 2012). Furthermore, birds in better body condition could arrive earlier and could occupy better territories (Kokko 1999), which is potentially an important asset in our study species (Lundberg et al. 1981; Wiggins et al. 1994). In this second step of the analyses, we used the same candidate set of SEM models for the causal relationships among the response variables.

The fit of all models was investigated with χ^2 test (Barrett 2007). Models were compared using the Akaike information criterion (AIC), but using other information criteria for model comparison gave very similar results (the Bayesian information criterion, AICc; results not shown). We considered models with AIC difference from the best model greater than 2 as having less support than the best model. However, models with an AIC difference greater than two may also have some support (Burnham et al. 2011); thus, we provide information on all models in the Supplementary material (Tables S5 and S6). We assessed the parameter weights by summing the weights of all models containing the focal path coefficient (Symonds and Moussalli 2011).

All statistical analyses were performed within the R 3.2.3 statistical environment (R Development Core Team 2015). Multi-response models were built using the 'MCMCglmm' package (Hadfield 2010), while the SEM analysis was done using the 'sem' package (Fox et al. 2015).

Results

Results from the model uncontrolled for the effect of body condition

The correlation matrix resulting from the MCMCglmm not accounting for the effect of body size and body condition yielded a moderately negative relationship between FID and number of chicks (posterior mode − 0.13, credible interval (− 0.20–0.06)), and a positive relationships between FID and survival to the next year (0.14, (− 0.19–0.44)) and between the life history variables (0.15, (− 0.14–0.45)). However none of these relationships could be discriminated statistically from zero based on the wide 95% credible intervals they were associated with (Supplementary Table S3).

Among the eight initial models considered in the first step of the analysis, two models reached similar support (Table 1). According to the best model (AIC = 13.74), there was a positive relationship between survival to the next year and the number of chicks (path coefficient ± standard error = 0.17 ± 0.06) and between FID and survival to the next year (0.16 ± 0.06). The other best-supported model (AIC = 15.28) was the model in which the three phenotypic traits were connected with a common latent variable, representing POLS. According to the cumulative AIC weights, there is 63% probability that one of the first two models is the best model. The variable weights of the paths represented in the models (Table 2) also indicate the importance of the positive relationships between survival to the next year and the number of chicks (variable weight = 0.63) and between FID and survival to the next year (0.56). The path coefficients and their standard errors are shown in Fig. 3 for the best-supported models and in Supplementary Table S5 for all of the models.

Results from the model controlling for the effect of body condition

Similarly to the above, the correlation matrix extracted from the MCMCglmm accounting for the effect of body condition contained a moderate negative relationship between FID and reproductive investment (posterior mode − 0.07, credible interval (− 0.21–0.06)), and positive ones between FID and survival to the next year (0.17, (− 0.19–0.43)) and between the life history variables (0.13, (− 0.12–0.48)). The 95% credible intervals associated with these estimates included zero (Supplementary Table S4).

In this step, the first two models were the same as the two best-supported models in the first step (AIC = 11.23, 12.21, Table 1). As indicated by the cumulative AIC weights, the best model is among the two models with the lowest AIC values with 77% probability. According to the variable weights, the positive relationships between survival to the next year and number of ringed chicks (variable weight = 0.53) and between survival to the next year and FID (0.65) were also important in this dataset (Table 2). We show the parameters of the two best-supported models in Fig. 3 and of all models in Supplementary Table S6.

Discussion

To evaluate the general predictions of the POLS hypothesis, we investigated the relationships between one behavioural and two life history traits by adopting a SEM approach to our long-term data collected from the collared flycatcher. The main results of our study were the following. Birds returning in the next year had more ringed offspring, and in agreement with the generally accepted predictions of the POLS, individuals taking higher risk had lower chance to survive. However,

Table 1 The results of the model selection based on our two model sets (not controlling and controlling for the effect of body size and body condition). The model numbers correspond to the numbers on Fig. 2. The number of estimated parameter, the logarithm of the model likelihood, the Akaike information criterion (AIC), the difference in AIC between the focal model and the best model, the AIC weights representing the probability of the focal model to be the best model and the cumulative version of the latter are shown

Model	Number of parameters	Log likelihood	AIC	ΔAIC	AIC weights	Cumulative AIC weights
Based on the model not accounting for body size and body condition						
6	5	− 1.87	13.74	0	0.43	0.43
1	5	− 2.64	15.28	1.54	0.20	0.63
5	5	− 2.96	15.92	2.18	0.14	0.77
7	5	− 3.45	16.89	3.15	0.09	0.86
2	4	− 4.83	17.66	3.92	0.06	0.92
3	4	− 5.32	18.63	4.89	0.04	0.96
4	4	− 5.63	19.27	5.53	0.03	0.99
0	3	− 7.50	21.01	7.27	0.01	1
Based on the model accounting for body size and body condition						
6	5	− 0.61	11.23	0	0.48	0.48
1	5	− 1.10	12.21	0.98	0.29	0.77
3	4	− 3.22	14.45	3.22	0.10	0.87
7	5	− 2.61	15.22	3.99	0.07	0.94
2	4	− 4.41	16.83	5.60	0.03	0.97
5	5	− 3.80	17.60	6.38	0.02	0.99
0	3	− 6.53	19.06	7.84	0.01	1
4	4	− 5.92	19.84	8.61	0.01	1

we found only a weak positive relationship between risk-taking behaviour and the number of ringed offspring. These relationships did not change substantially when we controlled for body size and body condition according to the asset protection hypothesis. These results only partly support the general predictions of the POLS hypothesis. On one hand, we derived supporting evidence by the finding that there is a negative relationship between risk-taking behaviour and survival to the next year. On the other hand, the fact that the relationship between survival to the next year and current reproductive effort is positive is against the predictions of the POLS hypothesis based on trade-offs. We found some support for a single latent trait to be responsible for the association between the three investigated traits, but we could not convincingly accept or reject this scenario with the available data.

The absence of a general POLS underlain by a trade-off in our study population is similar to the findings of other studies (Kluen et al. 2014; Royauté et al. 2015; Závorka et al. 2015). It has been suggested that the failure to find POLS mediating a relationship among traits might be due to the heterogeneity of environmental conditions (Závorka et al. 2015; Jäger et al. 2017), which may be the case in our study (Török et al. 2004; Hegyi et al. 2013). We intended to model this scenario in our second step, in which we controlled for body condition. However, it might be that some heterogeneity that is caused by the environment is not captured nor by body condition, neither by our other control variables, and thus remained unaccounted for in our statistical models. Therefore, we cannot exclude the scenario that a syndrome emerges in certain environmental conditions only (Bell 2005; Dingemanse et al. 2007), but we cannot investigate this possibility further with the available data. We note that our results are correlative and the obtained effect sizes are relatively low, and thus, in spite of the large sample size and the coverage of almost ten consecutive years of field work, they should be interpreted with caution. It should be mentioned that probably if we could capture all of the birds, also the shyest birds, the correlations would be stronger. Our results suggest at least that alternative causal

Table 2 Variable weights (summing the AIC weights of the models containing the focal path coefficient) from the two models (data not controlling and controlling for body size and body condition). Flight initiation distance (FID) is an inverse estimate of risk-taking

Number of chicks → survival to the next year	FID → survival to the next year	FID → number of chicks	Latent → survival to the next year	Latent → number of chicks	Latent → FID
Based on the model not accounting for body size and body condition					
0.63	0.56	0.26	0.20	0.20	0.20
Based on the model accounting for body size and body condition					
0.53	0.65	0.10	0.29	0.29	0.29

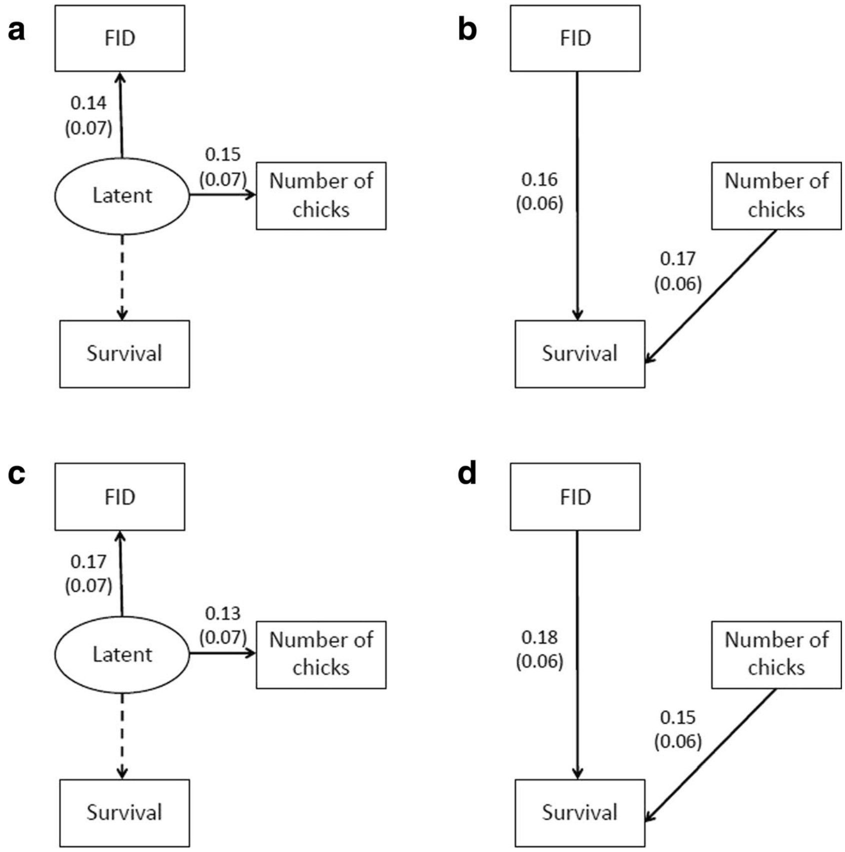

Fig. 3 The two best SEM models from the analysis not accounting for body size and body condition (**a**, **b**) and accounting for the body size and body condition (**c**, **d**) with the corresponding path coefficients and standard errors (in parenthesis)

mechanisms (and not necessarily a trade-off between current and future reproductive value)t?> are equally likely to mediate a relationship between the measured traits. Although we were unable to derive evidence for a life history trade-off, we could not reject the POLS hypothesis, because other mechanisms, like correlational selection or gene pleiotropy, could cause relationships between phenotypic variables fulfilling criteria for POLS (Sinervo and Svensson 2002; Sih et al. 2004). Furthermore, we cannot exclude the possibility that other behavioural traits are involved in POLS, or that unmeasured life history traits (e.g. next-year offspring production) are responsible for the trade-off between present and future reproductive value in our population; thus, such trade-offs remained unidentified in our study.

We failed to detect signatures of trade-off, which is generally stated to be the key mechanism generating POLS structure (Réale et al. 2010), as survival to the next year was weakly positively related to the current reproductive effort in our study. The magnitude of this connection is comparable with the correlation between the mean number of recruits per year and breeding lifespan (r_{sp} = 0.142) in our study population (Herényi et al. 2012). A possible explanation for this pattern is that the quality of the individual or the amount of resources the individual can acquire may confound life history trade-offs (van Noordwijk and de Jong 1986). Furthermore, our results are in accordance with the 'having it all' hypothesis (Johnston et al. 2006) or the 'silver spoon' effect, i.e. those individuals with good developmental conditions can achieve higher success later in life (Grafen 1988; Briga et al. 2017; Han and Dingemanse 2017). Additionally, in migratory and territorial animals, individuals arriving earlier could occupy better territories and could thus simultaneously achieve greater reproductive success and higher survival probability, coupled with a greater investment in territory defence (Lundberg et al. 1981; Wiggins et al. 1994; Kokko 1999; Scales et al. 2013). However, in our case, this latter explanation is unlikely, because we controlled for the effect of arrival date, and this variable had small effect on the response variables (Supplementary Table S7). Furthermore, the effect of survival probability and dispersal or permanent emigration could not be completely distinguished by our proxy value for survival (recapture probability in the next year), which might blur trade-offs for survival. Habitat selection, for example, is connected to previous reproductive success. Accordingly, differential dispersal may be the cause of the observed positive relationship between survival to the next year and current reproductive investment (Pärt and Gustafsson 1989; Doligez et al. 1999).

However, in our study species emigration is probably low, because the movements between plots are infrequent and dispersal is low (Pärt 1990; Garamszegi et al. 2004a).

There was a weak positive relationship between FID (an inverse measure of risk-taking behaviour) and survival to the next year in our data, indicating that birds taking less risk (having higher FID) are more likely to return in the next year than more risk-taking birds. Therefore, it seems that cautious birds invest more in survival or that individuals with higher future expectations are more cautious. This pattern is in agreement with previous meta-analytical findings indicating that risk-taking behaviour in males can be coupled with lower survival ($r = -0.11$, Smith and Blumstein 2008). Risk-taking behaviour may be negatively associated with survival to the next year not only because of the current-future reproductive value trade-off, but also through mechanisms driven by other trade-offs, for example between growth and mortality (Stamps 2007), or correlational selection caused by predation or parasite risk (Sinervo and Svensson 2002; Wolf et al. 2007; Møller 2008; Barber and Dingemanse 2010). However, if risk-taking behaviour is connected to dispersal, as found in fish (Cote et al. 2013), our results can be biased by risk-taking individuals dispersing further and being undetected.

We found little evidence for the relationship between risk-taking behaviour and current reproductive effort. The magnitude of this relationship was similar to that found in the abovementioned meta-analysis ($r = 0.10$, Smith and Blumstein 2008) and in barn swallows (*Hirundo rustica*) ($r = 0.13$, Møller 2014) and slightly lower than in a phylogenetic comparative analysis of birds (slope = 0.209, Møller and Garamszegi 2012). Reproductive success usually increases with risk-taking behaviour (see also Colléter and Brown 2011; Patterson and Schulte-Hostedde 2011), but sometimes the intermediate level of risk-taking leads to the highest success (de Jong et al. 2013), while other studies have not found any of these relationship (Cote et al. 2008; Brent et al. 2014). It is probable that in our species, mainly the characteristics of the female (e.g. age, condition through determining laying time and clutch size (Lundberg and Alatalo 1992) or behavioural type (Dingemanse et al. 2004)) or, having mutual mate choice and biparental care, the combined behavioural phenotype of the pair (which probably affect the cooperation of the pair) (Schuett et al. 2011; David et al. 2015), influence the number of offspring produced, in which the risk-taking behaviour of the male plays a minor and possibly undetectable role.

Because the SEM including body mass and body size revealed very similar output compared to the uncontrolled model, if the ‘having it all’, ‘silver spoon’ or ‘state-dependent safety’ hypotheses are true for our data (indicated by the positive relationship between survival to the next year and reproductive investment), it is unlikely that aspects of individual quality or the amount of resources an individual acquires that conceal the trade-off between life history variables are related to body size or body condition. Instead, assets may be connected to the quality of the territory, to experience or to the cognitive capacities of the individuals. For example, it is possible that males with good territories could afford to raise more offspring and still have higher probability to survive. According to the state-dependent safety hypothesis (Luttbeg and Sih 2010), we should expect that high-quality (indicated by higher survival probability and more offspring) birds could afford to take more risk, which was found in other systems (Godin and Davis 1995; Réale et al. 2009), but which is in contrast with our results. Furthermore, it is also possible that effects due to acquired assets are manifested in the relationship of life history traits but do not influence associations with risk-taking behaviour. Accordingly, good-quality birds may not need to take great risks to acquire and retain resources, to produce more offspring and to realize higher survival. We note that the existence of mechanisms driven by individual quality does not reject necessarily hypotheses that are based on trade-offs. It remains plausible that the amount of acquired assets is a confounding variable that masks the trade-off between current and future reproductive value (van Noordwijk and de Jong 1986; Chapman and Partridge 1996; Marden et al. 2003).

In conclusion, we found mixed support for the general predictions of the POLS hypothesis. Specifically, we found risk-taking behaviour to be negatively associated with survival to the next year, but the measured traits did not form a common syndrome through a latent variable that mediates life history trade-offs. However, we investigated only three variables, and other life history, physiological or behavioural traits may still follow the POLS structure. Our study similarly to other recent researches emphasizes the need of investigating POLS in a more nuanced way (Binder et al. 2016; Závorka et al. 2016). Future studies may benefit from exploring the influence of environmental and individual conditions, for example territory quality, on POLS in long-term datasets. There is a need for investigations of the potential mechanisms creating POLS based on data where within- and between-individual effects are separated.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. Permissions for the fieldwork have been provided by the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management, ref. no's: KTVF 16360-2/2007, KTVF 30871-1/2008, KTVF 43355-1/2008, KTVF 45116-2/2011, KTVF 21664-3/2011, KTVF 12677-4/2012 and KTVF 10949-8/2013, and was approved by the ethical committee of the Eötvös Loránd University (ref. no. TTK/2203/3).

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