Is flight initiation distance associated with longer-term survival in yellow-bellied marmots, *Marmota flaviventer*?

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The distance at which animals move away from threats, flight initiation distance (FID), is often used to study antipredator behaviour and risk assessment. Variation in FID is explained by a variety of internal and external biotic and physical factors, including anthropogenic activities. Most prior studies focused on unidentified individuals, so our understanding of the fitness consequences of FID is relatively limited. We asked whether consistent individual differences in variation in flight initiation distance is associated with variation in summer survival and/or winter survival in an individually marked population of yellow-bellied marmots. We found no clear association between flight initiation distance and summer survival or winter survival. This suggests that FID decisions, while demonstrably optimizing current survival, may not have longer-term fitness consequences. Our results may be explained by the relatively modest repeatability of FID or it may have emerged from our attempt to explain longer-term measures of fitness. Future studies of the fitness consequences of personality traits should pay particular attention to the time interval between measuring the individuality of a trait and examining its fitness consequences.

Flight initiation distance (FID) is a metric used to describe the distance at which animals flee from approaching threats (Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). FID is a common way to quantify antipredator behaviour, and FID studies have been conducted using a variety of taxa as study systems including birds (Møller, 2015), fishes (Samia et al., 2019) and lizards (Samia et al., 2016). We assume that FID will be optimized because it reflects an immediate economic decision. As Ydenberg and Dill (1986) pointed out, fleeing incurs both costs and benefits; thus, animals will monitor an approaching predator until fleeing provides an advantage. Fleeing from a threat may increase the probability of immediate survival, but it is a costly behaviour that often results in the loss of foraging or other opportunities. Conversely, not fleeing has a significant cost of a loss of future fitness due to predation (Cooper, 2015).

Flight initiation distance differs among species (Møller et al., 2014), but a variety of factors may influence the relative flightiness of individuals within a species. Group size, predator approach velocity, distance from burrow and escape substrate are all external

factors that can modify an individual's escape decisions (Blumstein et al., 2015). Internal factors such as body condition, stress hormone level (Seltmann et al., 2012), pregnancy status (Braña, 1993), body size (Møller, 2015) and body temperature (Rocha & Bergallo, 1990) can also affect FID. However, and importantly, FID can vary across individuals within a population (e.g. Allan et al., 2020) and across populations because of learning, local adaptation and genetic differences (Møller, 2015).

FID has been used to quantify 'boldness', which is a commonly studied aspect of an individual's temperament or personality (Réale et al., 2007). In animals, temperament is defined as individual differences in behaviour that remain consistent over time and across situations and are characterized by greater between-individual variation than within-individual variation (Réale et al., 2007). When FID is used as a measure of boldness, there is an inverse relationship between boldness and FID, with bolder individuals having shorter FIDs (Petelle et al., 2013). Traits such as boldness (as measured by FID) may influence survival. For instance, Smith and Blumstein's (2008) meta-analysis found that bolder individuals generally have greater reproductive success but shorter life spans, which was attributed to greater risk taking.

For species that have a highly seasonal life history, such as hibernators, predation risk is concentrated during the summer active

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season, while in the winter, there is a risk of starvation (French, 1990). Flighty animals may have a disadvantage in the winter when body condition is more important. However, in summer, flightiness can be key to avoiding predators and ensuring summer survival. On the other hand, flighty animals spend more time fleeing from predators and sacrifice opportunities to perform other fitness-enhancing activities, like foraging. Because of this significant trade-off, animals often delay their flight to continue with their activities (Ydenberg & Dill, 1986).

Almost all FID studies have been conducted on unidentified animals and, thus, are unable to account for the impact of individual differences on fitness consequences (Blumstein, 2019). Yellow-bellied marmots are an ideal system to study the survival costs of FID. We studied a population of individually marked marmots under continuous study since 1962 (Armitage, 2014; Blumstein, 2013). Prior studies in this system have shown that variation in other personality traits (aggression) has significant fitness consequences in terms of reproduction and recruitment (Armitage & Van Vuren, 2003). Importantly, we have shown that FID is individually specific (in at least some age cohorts) and varies by sex (Petelle et al., 2013). In pups, there are no individual differences in boldness, possibly due to a lack of experiences that would result in differentiation; however, there is individual variation in boldness in yearlings (Petelle et al., 2013). Previous sample sizes (70 adults) may have been too small to estimate significant repeatability in adults. During the summer active season, predation is the main source of mortality (Van Vuren, 2001) and predation risk has been shown to influence variation in temperament in other species (Brydges et al., 2008). Thus, we predicted that bolder individuals who, by definition, have relatively shorter FIDs, would also have reduced summer survival rates because these individuals have an increased risk of predation. We also predicted that shyer individuals with longer FIDs would have lower winter survival because these individuals spend less time foraging and gaining mass to prepare for winter hibernation.

METHODS

Study System and Site

Yellow-bellied marmots are 2–6 kg facultatively social sciurid rodents widely distributed throughout the western United States (Frase & Hoffmann, 1980). We studied marmots at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, U.S.A. (38°57′N, 106°59′W) during their summer active season (mid-April to mid-September; details in Blumstein, 2013; Philson & Blumstein, 2023). Marmots at the RMBL live in colony sites (geographically isolated locations) that may contain one or more social groups (groups of individuals that share burrows and interact with each other; Blumstein, 2013). We focused on marmots at six lower-elevation sites (River Annex, River, Bench, Horse Mound, Avalanche and the Gothic townsite) and six higher-elevation sites (Marmot Meadow, Cliff, Picnic, Boulder, North Picnic, Stonefield). Higher-elevation/up-valley sites have a shorter growing season and a suite of weather-induced life history differences (e.g. Blumstein, 2006; Maldonado-Chaparro et al., 2015; Van Vuren & Armitage, 1991). At these sites, hawks (*Buteo* spp.), golden eagles, *Aquila chrysaetos*, American badgers, *Taxidea taxus*, long-tailed weasels, *Mustela frenata*, and red foxes, *Vulpes vulpes*, are potential marmot predators (Van Vuren, 2001).

Trapping

Following Armitage (1982), marmots were trapped using walk-in live traps baited with horse feed set near burrow entrances or areas where marmots are observed. Once trapped, individuals were immediately transferred to cloth handling bags to record body mass, sex and reproductive status. Marmots were identified by uniquely numbered eartags that were inserted into the marmot's ears the first time it was captured, and a unique dye mark was painted on its dorsal pelage to permit identification from afar. The intensive capture protocol, coupled with near daily behavioural observations (Blumstein, 2013), ensured high detection probability, hence estimated apparent survival is likely close to the true survival probabilities (Ozgul et al., 2006). Nevertheless, males are more likely to disperse (Armitage, 2014); thus, a lower estimated apparent survival probability is expected for males.

Flight Initiation Distance

We estimated FID throughout the peak summer active season (late May through early August; Blumstein, 2013; Philson & Blumstein, 2023). Using a standard protocol (e.g. Blumstein et al., 2015), relaxed marmots (i.e. those not looking towards us in alarm) were approached in the field at a rate of 0.5 m/s. We prioritized experiments on solitary individuals but counted the number of conspecifics within 10 m if there were others. Prior work (Blumstein et al., 2015; Petelle et al., 2013) suggested that this measure of group size had a negligible effect on FID so we did not include it in the following analyses. We marked the location where the researcher began the approach by dropping a flag, then dropped flags at the location where the marmot became alert by looking around and marked the location where the marmot fled. We continued walking to the location where the marmot was initially observed and dropped a final flag. We used a metre tape to measure (to the nearest 0.01 m) the distance of each flag from the marmot's initial location. We recorded starting distance (the distance between the animal and the observer's starting point), alert distance (the distance between the observer and the animal when the animal oriented towards the observer), the distance at which the marmot initiated flight (FID) and the marmot's distance from the nearest burrow when it fled. We also noted the marmot's starting substrate (low vegetation, high vegetation, talus, dirt, stones), starting behaviour (sit, forage, look, rear look), slope of approach (measured in degrees), slope of flight (measured in degrees) and method of escape (run or walk).

The data set for FID contained 1052 observations collected between 2003 and 2020 from 308 individuals (125 males, 183 females). The FID measurements were conducted across the summer (mean ± SD = 29 June ± 19.8 days), with an average of 31.9 ± 12.1 individuals tested each year an average of 2.12 ± 0.64 times each. Almost all (94%) of the FID estimates were conducted before 1 August.

Relative Predation Risk

We classified predation risk as high or low using a predation index calculated by dividing the number of predators seen in a colony by the number of minutes spent observing that colony for that year (Pinho et al., 2019). We looked for predators whenever conducting behavioural observations throughout the field season (early May through early September). On average, we observed each colony area for 141.52 h each year and recorded an average of 146.13 predators across all colonies each year. Colonies were classified as high predation risk if the predator detection rate was above the median value observed across all colonies across all years.

Summer Survival

We inferred summer survival for those individuals seen or trapped after 1 August or seen in the following year. We only

included adults (those ≥ 2 years) in the data set because of some uncertainty quantifying survival for yearlings (many of which disperse). Our final summer survival data set contained 916 observations from 377 individuals (140 males, 237 females) from 2003 to 2020. When looking at both the summer survival and FID data sets together, the total number of individuals was 516, wherein 169 individuals (39 males, 130 females) were present in both data sets.

Winter Survival

Winter survival was inferred by determining whether the animal emerged from its annual bout of hibernation based on intensive field observations in the spring. For the winter survival data set, we used data from 2003 to 2019. Our final winter survival data set contained 1566 observations from 800 individuals (410 males, 390 females). When looking at both winter survival and FID data sets together, the total number of individuals present was 814, wherein 294 individuals (118 males, 176 females) were present in both data sets.

Statistical Analysis

We calculated the repeatability of FID using a data set that contained the 1052 observations from 308 unique individuals by using the 'rptR' package (Stoffel et al., 2017) in R (R Core Team, 2022). To calculate an individual's overall repeatability of FID, we included the following fixed effects (starting distance, sex, age, FID trial number, valley location and distance to burrow) and random effects (year, marmot unique identity). We also calculated an individual's overall repeatability of FID for each sex separately. We fitted data for only males or only females into two separate repeatability models that included the same fixed effects (minus sex) and random effects. We fitted bivariate models (Gao et al., 2017) to study the among-individual correlation between FID and summer survival and FID and winter survival that we describe in more detail below. Bivariate models jointly analyse each dependent variable (FID, summer survival, winter survival) as a function of a set of predictors, then estimate the correlated residual variances of traits that are not explained by primary predictors. This permits us to estimate among-individual correlation between traits to see whether individuals with overall higher FID (after accounting for primary predictors) have reduced or enhanced survival. While the use of multivariate models is common for estimating covariances for Gaussian or other continuous traits (Van de Pol, 2012), these models can also be used to estimate among-individual variances of binary traits such as survival (Hamel et al., 2012), as well as covariances between these traits (Bonnet & Postma, 2016; Cam et al., 2002, 2013; Knape et al., 2011; Paterson et al., 2018).

Summer Survival and FID

The general formula of our bivariate model is given below. We modelled the log FID using a Gaussian distribution and included the log starting distance (SD), sex, valley location (down valley/up valley), trial number, distance to burrow and age as predictors. We also included three random effects (colony, year, individual marmot identity).

All continuous variables were scaled before analysis (mean-centred and divided by their standard deviation). The βs represent regression coefficients, μ_0 represents the global intercept of the model, and ε represents the residual variance.

$$\mathrm{Log}(\mathrm{FID}_i) \sim N(\mu_i, \varepsilon)$$

$$\mu_i = \mu_0 + \beta_1 \log(\mathrm{SD}_i) \cdots + \beta_x \mathrm{age}_i + \mu^{\mathrm{FID}}_{\mathrm{year}[t]} + \mu^{\mathrm{FID}}_{\mathrm{individual}[i]}$$

We modelled summer survival using a Bernoulli distribution and included predator index, valley location (down valley/up valley), sex and age as predictors in addition to a colony random intercept, a year random intercept and an individual random intercept.

$$\mathrm{Summer\ survival}_i \sim B(\phi_i)$$

$$\mathrm{Logit}(\phi_i) = \mu_0 + \beta_1 \mathrm{predator\ index}_i \cdots + \beta_x \mathrm{age}_i + \mu^{\mathrm{SS}}_{\mathrm{year}[t]}$$
$$+ \mu^{\mathrm{SS}}_{\mathrm{individual}[i]}$$

We estimated the among-individual relationship between FID and summer survival by modelling the individual random intercepts as correlated, drawing them jointly from a multivariate normal distribution and estimating the covariance matrix $\sum$, with $\rho_{\mathrm{FID,SS}}$ representing the among-individual correlation between FID and summer survival.

$$\begin{bmatrix} \mu^{\mathrm{FID}}_{\mathrm{individual}} \\ \mu^{\mathrm{SS}}_{\mathrm{individual}} \end{bmatrix} \sim \mathrm{MVN}\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \sum \right)$$

$$\sum = \begin{bmatrix} \sigma^2_{\mathrm{FID}} & \sigma_{\mathrm{FID}}\sigma_{\mathrm{SS}}\rho_{\mathrm{FID,SS}} \\ \sigma_{\mathrm{FID}}\sigma_{\mathrm{SS}}\rho_{\mathrm{FID,SS}} & \sigma^2_{\mathrm{SS}} \end{bmatrix}$$

Weakly informative priors were used for all model parameters. We specified the following:

$$\sum \sim \mathrm{LKJ}(1)$$

$$\beta \sim N(0, 1.5)$$

$$\mu_0 \sim N(0, 3)$$

$$\mu_{\mathrm{individual}}, \mu_{\mathrm{individual}} \sim N(0, 1)$$

We computed the standardized linear selection gradient β_s, following Dingemanse et al. (2021), as:

$$\beta_s = \frac{C_{\mathrm{FID,SS}}}{\sigma^2_{\mathrm{FID}}} \frac{\sigma_{\mathrm{FID}}}{\phi}$$

With $C_{\mathrm{FID,SS}}$ being the among-individual covariance between the two traits and our fitness measure ϕ being the population mean summer survival. We also analysed the data using the same model but using only data from males or only data from females.

Winter Survival and FID

We estimated the relationship between winter survival and FID using a bivariate model whose structure was similar to the previous bivariate model. Winter survival was modelled using a Bernoulli distribution. We included prior August mass, valley location (down valley/up valley), date of first bare ground at a weather station at the RMBL, sex and age as fixed effects. For FID, fixed effects were the same as in the previous model: log(SD), distance to burrow, sex, age, valley location and trial number. We also included three random effects (colony, year, individual marmot identity). In

Table 1
Results of the bivariate model looking at the relationship between summer survival and flight initiation distance (FID), using the complete data set comprising both males and females

	Explanatory variable	Mean estimate	95% CI
Summer survival	Intercept	2.61	1.86, 3.63
	Low predation[a]	0.19	−0.36, 0.76
	Up valley[b]	−0.49	−1.37, 0.23
	Male[c]	−1.39	−2.20, −0.76
	Mass	0.58	0.28, 0.91
	Age	−0.49	−1.07, −0.05
Log(FID)	Intercept	3.02	2.63, 3.39
	log(SD)	0.54	0.49, 0.60
	Up valley[b]	0.36	−0.20, 0.93
	Distance from burrow	0.12	0.08, 0.17
	FID trial number	−0.07	−0.11, −0.04
	Male[c]	−0.07	−0.18, 0.04
	Age	0.01	−0.05, 0.06
Among-individual correlation	ρ	0.21	−0.41, 0.86

CI: credible interval. All continuous variables were scaled.
[a] Reference category is 'high predation'
[b] Reference category is 'down valley'
[c] Reference category is 'female'

addition, we conducted the same analysis described above using only data from males and data from females.

We fitted the statistical models in a Bayesian framework in R version 4.1.2, with the R package 'brms' version 2.16.3 (Bürkner, 2017), using Hamiltonian Monte Carlo simulations in 'Stan' (Carpenter et al., 2017). For all the models, we used two chains running for 10 000 iterations, including a burn-in period of 5000 iterations. We assessed convergence and mixing of the chains using the Gelman−Rubin diagnostic (Gelman & Rubin, 1992) with potential scale reduction factors all inferior to 1.02. The posterior predictive checks showed high correspondence between the observed data and data simulated under the statistical models, highlighting a good fit.

Ethical Note

Marmots were studied under the University of California, Los Angeles Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and under permits from the Colorado Division of Wildlife (TR917, renewed annually). Marmots were live-trapped and marked to facilitate observations. Traps were set in the morning and late afternoon (only when it was cool) and checked within 2 h of setting. Trapped marmots were processed quickly (within 5−15 min depending upon what needed to be done) and released at the point of capture. Prior work has shown that only those individuals that struggle in the trap (relatively few of them) have an increased glucocorticoid response (Smith et al., 2012). The majority of trapping events were with relaxed individuals. These trapping methods have been used for 61 years at the study site and there is no detectable effect on population viability. Flight initiation distance experiments caused many marmots to retreat temporarily into their burrows. Prior work has shown that some marmots habituate to repeated experimental approaches (e.g. Uchida & Blumstein, 2021), but we have no indication that this has fitness consequences (indeed, the results of this study suggest that FID does not have substantial long-term fitness consequences). Observations were conducted at distances that did not obviously interfere with marmot behaviour, which varied by group. Marmots have been regularly observed at this site for the past 61 years.

RESULTS

Repeatability of FID

Overall, adult repeatability of FID was significant, but modest ($R = 0.132$, 95% credible interval (CI) = [0.072, 0.195]). Repeatability of FID was significant when exploring females ($R = 0.154$, 95% CI =
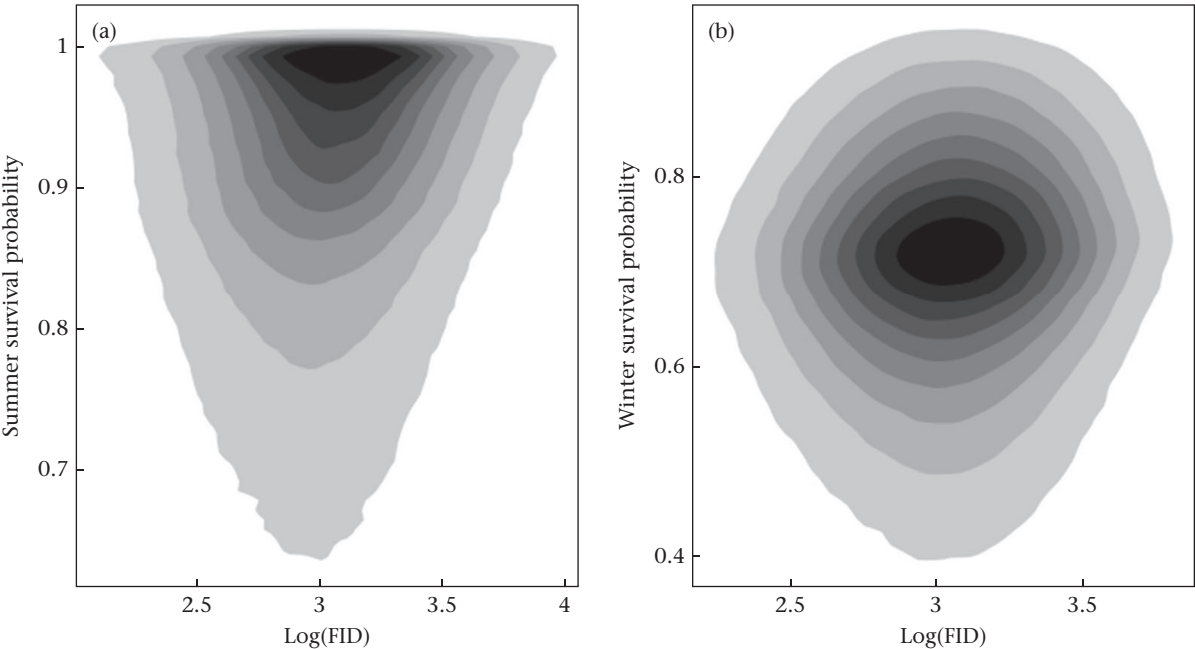

Figure 1. (a) Probability contours of the joint posterior distribution of summer survival probability and log flight initiation distance (FID) estimated from the bivariate model, showing the lack of clear among-individual correlation between both variables. (b) Probability contours of the joint posterior distribution of winter survival probability and log flight initiation distance estimated from the bivariate model, showing the lack of clear among-individual correlation between both variables. In both graphs, the contours delimit regions of probabilities from 0.1 (darkest colour; 10% of estimated values around the mean estimate contained within it) to 0.9 (lightest colour; 90% of estimated values contained within it).

[0.085, 0.227]) and males separately ($R = 0.150$, 95% CI = [0.017, 0.295]).

Flight Initiation Distance and Summer Survival

We found no clear among-individual correlation between flight initiation distance and summer survival using the complete data set ($r = 0.21$, 95% CI = [−0.41, 0.86]; Table 1, Fig. 1a) or when partitioning between sexes (males: $r = 0.34$, 95% CI = [−0.55, 0.95]; females: $r = 0.14$, 95% CI = [−0.85, 0.94]; Table 1).

Flight Initiation Distance and Winter Survival

Similarly, we found no clear among-individual correlation between flight initiation and winter survival using the complete data set ($r = 0.13$, 95% CI = [0.51, 0.86]; Table 2, Fig. 1b) or when partitioning between sexes (males: $r = 0.18$, 95% CI = [0.86, 0.95]; females: $r = 0.12$, 95% CI = [−0.84, 0.91]; Table 2).

DISCUSSION

Taken together, while FID has demonstrably been shown in many studies to be optimized for short-term flight decisions (e.g. Cooper & Blumstein, 2015), we found no support for the general hypothesis that these short-term decisions influenced summer or winter survival in a well-studied marmot population. This was somewhat surprising because FID is a metric typically used to quantify boldness, a repeatable personality trait, and meta-analyses have found that there are fitness consequences for personality traits (Smith & Blumstein, 2008). However, a more recent meta-analysis studying the relationship between personality and survival found no consistent association between riskier behaviours, measured in a variety of ways, and higher mortality (Moiron et al., 2020).

One reason for a failure to find a fitness consequence of FID is that humans may not pose a substantial predation risk to marmots. Indeed, few marmots are currently hunted in our valley. Yet, marmots respond to humans and modify FID with repeated approaches (Uchida & Blumstein, 2021), suggesting that they are able to learn to tolerate nonthreatening human approaches and that there is indeed some perceived risk associated with humans approaching them. Related to this, it is also possible that human-induced FIDs are not associated with predator-induced FIDs. This is a difficult question to study in our system because of the difficulty of developing a large data set of predator-induced FIDs. Nevertheless, marmots do respond to approaching humans, and we have

capitalized on this in the past to gain a number of meaningful insights about risk assessment (e.g. Blumstein et al., 2018; Morgan et al., 2021; Petelle et al., 2013; Uchida et al., 2022).

While the propensity to flee may be an individually specific trait, the consequences of this trait are often difficult to identify. The time at which a personality trait is measured and the time at which the fitness consequence of a given trait is measured may influence the magnitude of the correlation between the trait and its putative consequences. Furthermore, the setting (laboratory versus natural) and the study system could impact the findings of studies examining the personality–survival relationship. While individual variation in FID may influence variation in survival, the effect could be small and the variation better explained by a variety of other factors.

The surprising lack of clear correlation between FID and survival in our study may also be attributed to the relatively modest levels of repeatability in our study system. While previous studies of the repeatability of FID in marmots, using a substantially smaller data set, found that while it was significantly repeatable in yearlings, it was not repeatable in juveniles or adults (Petelle et al., 2013). With this larger sample size, we found modest, but significant, repeatability of FID in adults. Other studies that found significant negative correlations between individually specific FIDs and longer-term measures of survival had moderate ($R = 0.11$, Niemelä et al., 2015) to high ($R = 0.62$, Møller, 2014) repeatability estimates. Even in cases where repeatability is low, but significant, like ours, long-term studies provide the opportunity to explore the drivers and consequences of FID in a variety of contexts, adding more context to the biology of these animal systems.

When comparing our study with previous studies (Jablonszky et al., 2018; Møller, 2014; Niemelä et al., 2015; Santos et al., 2015), the time between when FID and survival were measured varied. In three of these four studies, individual survival was measured within 1 year of when the researchers measured FID. Only one of the studies, Møller (2014), measured long-term survival in the population using a survival data set that spanned 1980–2013 and FID data collected during 1982–2013.

Taken together, it is likely that the long duration over which we studied survival, combined with the modest repeatability (contra the high repeatability in Møller's (2014) study), in this system explains our failure to detect clear associations. This highlights an important challenge of studying the fitness consequences of personality traits: significant repeatability and a sufficiently large effect size. Smaller effects might permit the study of more immediate measures of fitness, but larger effects might be essential to study longer-term measures of fitness.

Table 2
Results of the bivariate model looking at the relationship between winter survival and flight initiation distance (FID), using the complete data set comprising both males and females

	Explanatory variable	Mean estimate	95% CI
Winter survival	Intercept	0.84	0.40, 1.23
	Date of snowmelt	−0.15	−0.38, 0.08
	August mass	0.41	0.23, 0.58
	Up valley[a]	0.12	−0.32, 0.61
	Male[b]	−1.42	−1.78, −1.09
	Age	0.01	−0.23, 0.21
Log(FID)	Intercept	3.03	2.65, 3.40
	log(SD)	0.54	0.49, 0.60
	Up valley[a]	0.37	−0.20, 0.94
	Distance from burrow	0.13	0.08, 0.17
	Trial number	−0.07	−0.11, −0.04
	Male[b]	−0.08	−0.19, 0.04
	Age	0.01	−0.04, 0.06
Among-individual correlation	ρ	0.13	−0.51, 0.86

CI: credible interval. All continuous variables were scaled.
[a] Reference category is 'down valley'
[b] Reference category is 'female'

It is also possible that boldness could be beneficial in certain contexts (e.g. resource acquisition) but costly in others (e.g. in relation to predation). When looked at over multiple years, these impacts could balance out and reduce the effect size. Additionally, the among-individual correlation could vary in different environmental contexts and environmental variation could further reduce its effect.

While studies in the field enhance ecological validity, they limit the possibility of controlling for other environmental factors that affect behaviour. Since all our data were collected over many years from this detailed field study, the variance created by this could partially explain our results. Life history drivers such as valley position or sex may be more important than FID in explaining survival differences and provide a reason for our lack of correlation. Differences in individual quality may also be a reason why our results do not show the trade-off or negative correlation that we expected. Individuals acquire and allocate resources differently, leading to poor-quality and high-quality individuals (Van Noordwijk & de Jong, 1986). The unaccounted for variation in the quality of the individuals in our data set may be more important in driving survival trends rather than the modest consistent variation in temperament.

To some extent, studying the fitness consequences of individual differences parallels a common problem of studying the fitness consequences of specific ontogenetic experiences such as play behaviour (Bekoff, 1988; Burghardt, 2005). It is difficult to deprive animals of key experiences, and much can happen between the time a measure is estimated and the time its consequences are quantified. Interestingly, a prior study in the marmot system showed that play had significant relationships with later dominance, but the effect dissipated over time (Blumstein et al., 2013). Importantly, for a trait like flight initiation distance, where many immediate contextual variables explain substantial variation, consistent individual differences may have limited variation to explain. Future studies should explicitly study the effect of the duration between when the individuality of a trait is measured and the consequences of that trait.

Author Contributions

D.T.B. designed the study and managed the project. D.T.B. and C.S.P. collected data. C.S.P. put together the data sets from archival data. L.B. led the analysis which was conducted with M.S. M.S. and D.T.B. wrote the first draft of the paper with specific contributions by C.S.P. and L.B. All authors critically contributed to drafts and gave final approval for publication.

Data Availability

Data and code to reproduce these analyses are available at https://osf.io/3wy58/.

Declaration of Interest

None.

Acknowledgments

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Appendix

Table A1
Results of the bivariate models looking at the relationship between summer survival or winter survival and flight initiation distance (FID), using data sets comprising only males or females

	Explanatory variable	Mean estimate	95% CI
Summer survival, males	Intercept	1.62	0.56, 2.85
	Low predation[a]	−0.09	−1.01, 0.84
	Up valley[b]	−0.50	−1.76, 0.73
	Mass	0.42	−0.11, 0.97
	Age	0.26	−0.49, 0.94
Log(FID), males	Intercept	2.77	2.07, 3.36
	log(SD)	0.60	0.48, 0.71
	Up valley[b]	0.35	−0.55, 1.34
	Distance from burrow	0.14	0.06, 0.23
	Trial number	−0.09	−0.16, −0.01
	Age	−0.08	−0.21, 0.05
Among-individual correlation, males	ρ	0.34	−0.55, 0.95
Summer survival, females	Intercept	2.17	1.54, 2.98
	Low predation[a]	0.29	−0.31, 0.91
	Up valley[b]	−0.34	−1.19, 0.37
	Mass	0.61	0.27, 0.95
	Age	−0.49	−1.00, −0.15
Log(FID), females	Intercept	3.06	2.71, 3.40
	log(SD)	0.52	0.46, 0.59
	Up valley[b]	0.38	−0.15, 0.93
	Distance from burrow	0.11	0.06, 0.17
	Trial number	−0.07	−0.11, −0.02
	Age	0.03	−0.03, 0.09
Among-individual correlation, females	ρ	0.14	−0.85, 0.94
Winter survival, males	Intercept	−0.32	−0.87, 0.11
	Date of snowmelt	−0.12	−0.34, 0.08
	August mass	0.16	−0.11, 0.44
	Up valley[b]	0.14	−0.41, 0.78
	Age	0.61	0.27, 0.95
Log(FID), males	Intercept	2.81	2.09, 3.37
	log(SD)	0.60	0.48, 0.71
	Up valley[b]	0.34	−0.57, 1.30
	Distance from burrow	0.15	0.06, 0.23
	Trial number	−0.09	−0.16, −0.01
	Age	−0.06	−0.17, 0.05
Among-individual correlation, males	ρ	0.18	−0.86, 0.95
Winter survival, females	Intercept	0.80	0.25, 1.29
	Date of melt	−0.16	−0.46, 0.14
	August mass	0.36	0.17, 0.55
	Up valley[b]	0.02	−0.58, 0.65
	Age	−0.11	−0.36, 0.09
Log(FID), females	Intercept	3.05	2.70, 3.40
	log(SD)	0.52	0.46, 0.59
	Up valley[b]	0.37	−0.15, 0.92
	Distance from burrow	0.11	0.06, 0.17
	Trial number	−0.07	−0.11, −0.02
	Age	0.03	−0.03, 0.09
Among-individual correlation, females	ρ	0.12	−0.84, 0.91

CI: credible interval. All continuous variables were scaled.
[a] Reference category is 'high predation'.
[b] Reference category is 'down valley'.