



Parent personality is linked to juvenile mortality and stress behavior in the arctic fox (*Vulpes lagopus*)

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Abstract

Life history theory predicts that individuals will differ in their risk-taking behavior according to their expected future fitness. Understanding consequences of such individual variation within a behavioral trait is crucial in explaining potential trade-offs between different traits and in predicting future dynamics in changing environments. Here, we studied individuals in a wild arctic fox population to explore if (1) individual variation in risk-taking behaviors of adult arctic foxes and in stress-dealing behaviors of their juveniles exist and are consistent over time to verify the existence of personality traits; (2) those behavioral traits in adults and juveniles are correlated; (3) they can explain fitness-related components (i.e., juvenile physical condition, mortality rate). We presented simple field experiments assessing behavioral traits by observing adult reactions toward approaching observers, and juvenile behaviors while trapping. Through the experiments, we found highly consistent individual variation of adults in vigilance and boldness levels, and more flexible juvenile behavioral traits categorized as investigating, passive, and escaping. The offspring of bolder adults exhibited more investigating behaviors and were less passive than the offspring of shy adults. Juvenile physical condition was not related to their mortality nor any behavioral traits of either parents or themselves. Lastly, highly investigating and active juveniles with bold parents had significantly lower mortality rates. This shows that interactions between parent personality and juvenile behavioral traits affect a fitness-related component in the life history of individuals.

Significance statement

The recent surge of interest in consistent individual difference in behavior, also called as animal personality, has already focused on its fitness consequences, but few studies have investigated the interactions between parent and offspring personality, and their ecological consequences. Moreover, this has rarely been studied in wild canids. The arctic fox is a charismatic species showing wide individual variation in behaviors. They live in highly fluctuating tundra ecosystems providing different selection regimes, making it even more eco-evolutionarily intriguing. Yet, few studies looked into behavioral traits and their importance in this system. While introducing simple methods to improve personality research in the wild, we provide a unique example of how variation in both parents and their juveniles collectively works for group dynamics in a cyclic population. This provides a firm basic for understanding behavior-mediated dynamics and opens up broader questions on how fluctuating environments exert varying pressures on individual differences.

Keywords Animal personality · Individual variation · Fitness · Risk-taking behavior

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Introduction

Individual variation within a population can lead to decoupled responses of individuals from a population under particular conditions (Bolnick et al. 2003, 2011). One aspect of phenotypic variation is personality, which can be defined as an individual's behavioral trait that is consistent over time and context (Sih et al. 2004). This consistency in behavior limits behavioral plasticity of individuals and affects how they respond to potential risks (Bremner-Harrison et al. 2004; Both et al. 2005; Smith and Blumstein 2008). Such individual differences in individual personality might be related to (1) a trade-off between two ends of a personality spectrum where, for example, bold individuals could have a higher reproductive success but lowered survival rates; or (2) changing environmental conditions shifting selective regimes on personalities (Both et al. 2005; Dingemans and Réale 2005; Smith and Blumstein 2008). Personality could also mediate population dynamics, interactions, and predator-prey relationship where individual variance could alter the structure and degree of interactions in the community networks, or even stabilize a given population in fluctuating environments by avoiding intraspecific competition (Bolnick et al. 2011; Hart et al. 2017).

The consequences of individual variation in behavioral traits are of particular concern in endangered populations in fluctuating environments. For instance, such variation could alter predation risk and destabilize predator-prey interactions compared to when treating all individuals as identical in responding to the same external stimuli. Although many studies have recently emphasized ecological consequences of individual differences, few studies have tried to test the underlying mechanisms of such consequence of individual variation and a potential interplay of personality traits between parents and their juveniles (Stankowich and Blumstein 2005; Smith and Blumstein 2008; Cole and Quinn 2014; Arroyo et al. 2017). This might be due to difficulties in measuring personality traits directly related to risk-taking strategies in the wild and in linking them to fitness consequences. Interactions between parent and juvenile behavior traits also remain poorly understood despite the importance to components explaining extended effects of personality at the very fine scale.

Scandinavian arctic foxes (*Vulpes lagopus*) live in highly fluctuating subarctic environments triggered by the cycle of their prey base, lemmings (*Lemmus lemmus*), and voles (*Microtus agrestis* and *Myodes* spp.) (Elmhagen et al. 2000; Meijer et al. 2013). Lemmings undergo population cycles every 3 to 5 years that can be divided into three phases—increase, peak, and decrease (Angerbjörn et al. 2001). Many other predators are also tied to the rodent cycle, from small mustelids to top predators such as wolves (*Canis lupus*) and golden eagles (*Aquila chrysaetos*) (Gilg et al. 2003; Ims and Fuglei 2005). During a drastic population decline in the rodent population, a crash, intraguild predation increases in this

community. In such an extremely fluctuating environment, a population is likely to experience changing selection regimes and individuals with different strategies within the same population (Dingemans et al. 2004; Both et al. 2005; Haage et al. 2017). Individual variation in personality and other behavioral traits with consequences for fitness could thus affect the dynamics of the endangered arctic fox population.

We propose that the arctic fox is a suitable model to study individual behavioral variation since (1) it is possible to conduct in-depth behavioral studies thanks to the 24 h visibility during tundra summers, den accessibility, and high tolerance toward human observers; (2) they live in a fluctuating environment with different selection pressures providing an eco-evolutionarily interesting system; (3) understanding different fitness consequences of personality would be important in the conservation of endangered Scandinavian arctic fox populations and could be used in the ongoing reintroduction program (Bremner-Harrison et al. 2004; Angerbjörn et al. 2013; Haage et al. 2017).

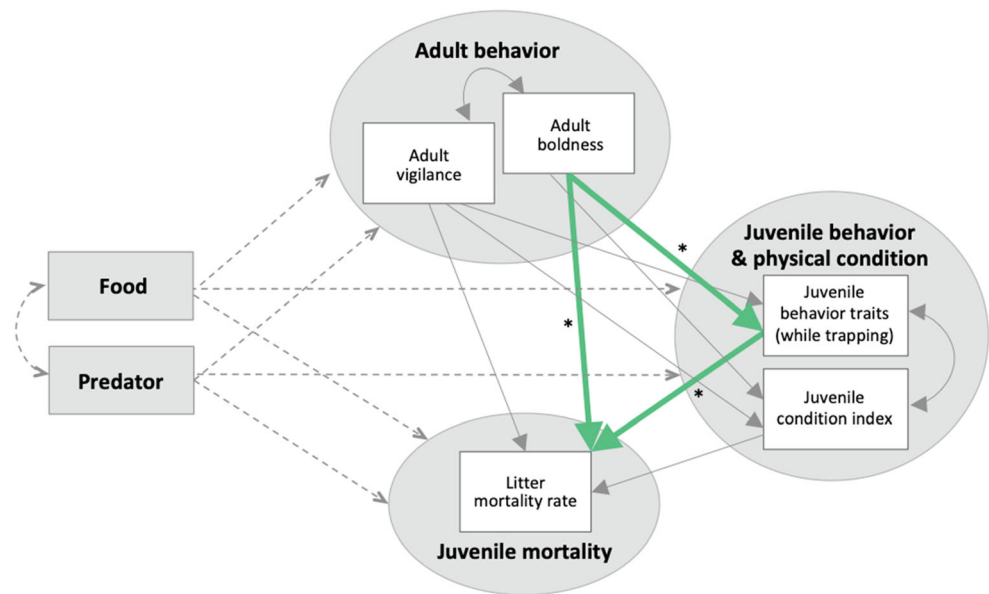
In this study, we investigated individual variation in personality and behavioral traits of adult and juvenile arctic foxes in Sweden and the relation of this behavioral variation to juvenile mortality and physical condition. We conducted novel experiments simulating risk and stress factors both for adults and juveniles to assess individual responses to risky and challenging situations in which personality could be strongly expressed (Koolhaas et al. 1999; Zozulya et al. 2008). In this context, we raised questions to disentangle the complex processes regarding the fitness of arctic foxes in terms of adult and juvenile behavioral traits. Here we investigated whether (1) individual variation in risk-taking behaviors of adult arctic foxes and in stress-dealing behaviors of their juveniles exist and are consistent over time to verify the existence of personality traits; (2) those behavioral traits in adults and juveniles are correlated; (3) they can explain fitness-related components (i.e., juvenile physical condition, mortality rate; Fig. 1). This in-depth study on the behaviors of adult and juvenile foxes in the wild and their consequences on fitness-related components aims to provide a better understanding on how individuals within a population would differ in responding to the dramatically shifting, yet synchronized, environmental changes.

Material and methods

Study population

This study was conducted in two mountain tundra areas, Vindelfjällen (66° N, 16° E) and Helags (63° N, 12° E) in North-western Sweden. Arctic foxes prey mainly on lemmings, voles and occasionally on bird species including ptarmigan (*Lagopus muta* and *L. lagopus*) and scavenge carcasses of other animals such as reindeer (*Rangifer tarandus*)

Fig. 1 Summary of the relationships between adult personality (vigilance and boldness), juvenile behavior traits, physical condition, and juvenile mortality. All lines are tested statistically and dashed lines are food and predator proxies provided in the study (see Appendix for details). The thick starred lines represent statistically significant relationships ($p \leq 0.05$) and the major pathway found in the study



(Elmhagen et al. 2000). They mostly live as a breeding pair but also form complex groups with additional related adults in a den (Elmhagen et al. 2014). The predator species which prey on arctic foxes are golden eagle, wolverine (*Gulo gulo*), red fox (*Vulpes vulpes*), white-tailed eagle (*Haliaeetus albicilla*), and brown bear (*Ursus arctos*) (Tannerfeldt et al. 1994). In both areas, a conservation program provides arctic foxes with supplementary feed (dog food) and carries out lethal control of red foxes (Angerbjörn et al. 2013).

Arctic foxes use specific and well-known den sites that are reused by generations of foxes over many decades (Elmhagen et al. 2014). In the study areas, the whole population has been monitored since 1980s in Vindelfjällen and since 2000 in Helags and the majority of the foxes was ear-tagged and genetically analyzed (Hasselgren et al. 2018). We visited all known den sites to monitor the presence of arctic foxes and their reproductive status from July to August in 2015. At dens with juveniles, we further observed the den for at least a continuous 24 h period at 150–300 m distance to collect behavioral data and estimate litter sizes. We then trapped juveniles using baited wire live traps (Tomahawk), recorded their sex, weight, hind foot length, and ear-tagged them to be able to recognize individuals for conservation purposes. When a juvenile was trapped, we recorded behavior of the individual from a distance before approaching the trap. We also recorded behavior of an adult reacting toward human approaching the den when juveniles were present. We were able to determine the parentage of a litter even in a complex group with the combination of field observations and individual information from the monitoring in previous years. We revisited occupied dens during the study period for further monitoring of survival

and behaviors. We also used camera traps (Ltl acorn) at some dens to gain more behavioral and survival data. Recording data blind was not possible since the study involved focal animals in the field.

Juvenile mortality rate, litter size, and condition index

We estimated the rate of mortality by comparing the minimum number of juveniles between the first and subsequent visits. Arctic fox juveniles start to emerge at the den in late June and can disperse later in the autumn by around September (Angerbjörn et al. 1995). Juveniles mostly appear above ground every day after weaning (Angerbjörn et al. 1995), meaning that juveniles not seen during a period of at least 24 h of continuous observation are likely to have died. Subsequent visits were normally after 1 or 2 weeks, and we standardized the periods to one week. Thus, weekly den-level mortality rate was defined as the proportion of juveniles not observed on subsequent visit 1 week later and hence assumed to be dead.

The litter size was estimated as the total number of observed juveniles during at least 24 h of observation in each visit. We could also combine ear-tags, fur color, and camera trap data to better estimate the litter size. At two dens where more individuals were counted at the last visit than at the first visit, the mortality rate was assumed to be zero.

Hind foot length and weight of individual arctic foxes measured from trapping were used to calculate the condition index (K) of an individual as below:

$$K = W / (a \times L^b)$$

W is weight, L is hind foot length, coefficient a was set to 0.416 and b to 1.708 following a previous study on the arctic fox (Tannerfeldt et al. 1994).

Human approach test for adult personality

We tested risk-taking reactions from adult arctic foxes ($n = 17$). Two human observers approached the den when an adult was present with their juveniles, starting from 100 m (measured using a GPS) and stopping every 20 m for 30 s. During the 30 s, we recorded the presence or absence of responsive behaviors of adults (i.e., binomial one-zero sampling). Definitions of behaviors recorded in the ethogram are shown in Table 1. We also included the initiation distance for behaviors of interests (i.e., barking, fleeing, relaxing) as latency data, which is known to be important in antipredator behaviors (Stankowich and Blumstein 2005). To account for latency, behavior scores were weighted according to the distance of the observer from the den; a behavior observed at 100 m scored 6 points, 5 points for 80 m, 4 points for 60 m, etc., 1 point for 0 m, and 0 point if the behavior was not observed. All points were summed by behavior to create a total point for each behavior of an individual.

Behavior observation of trapped juveniles

We trapped 193 juveniles out of 234 individuals counted in total in two study areas. Among them, we observed risk-related behaviors of 104 juveniles when they were exposed to a stressful, novel situation in a trap. In some cases, we could not observe the behavior of trapped juveniles when, for examples, the weather was not suitable for observation, or when more than two cubs were trapped at the same time. We kept the traps under constant observation after the traps were set from the tent at about 200–300 m. When a cub was trapped, we recorded 3 min of continuous frequency sampling or 30 s interval binomial sampling observations. We employed the latter sampling method for additional fieldworkers as it requires less training and experience to do and has been proved to provide broadly similar results in this behavior experiment (Grocutt 2015). We standardized the two methods by group mean and standard deviation to correct for different scales for our analyses. In the continuous frequency sampling, we recorded the frequency of all behaviors the cub displayed (Table 1) continuously for 3 min. Whenever the cub changed its behavior, we recorded it, and those

Table 1 List of behaviors exhibited by adult arctic foxes at the den while observers approaching them (i.e., human approach) and by trapped juveniles (modified from Grocutt 2015) that were recorded in

an ethogram during data collection. Asterisks indicate behaviors that were combined for principal component analysis

Behavior	Definition
Human approach	
Warning bark	Short loud bark toward a potential danger
Watching observer	Looking at the observer often with vigilance
Hiding	Moving out of sight into a den hole or somewhere invisible to avoid a potential danger
Watching side	Looking around with vigilance
Fleeing	Running toward den or away from a potential danger
Walking around	Slow gait of locomotion
Lying down	Lying or sleeping in a relaxed or asleep posture, ears normally lowered.
Standing	Standing still without moving around
Sitting	Sitting on hind quarters
Trapped behaviors	
Lying down	Lying or crouching low in the trap
Moving around	Moving around within the trap, on all fours or while crouching
Digging	Digging at the door or on the bottom of the trap
Scratching sides	Scratching or pawing at the sides of the trap
Biting trap	Biting or attempting to place its teeth around any part of the trap
Standing still	Standing on all fours without moving around
Sniffing	Sniffing at the trap or the air
Pshing	Pushing or applying body weight to the sides of the trap with its paws
Eating	Eating or other masticatory behaviors involving the bait in the trap
Sitting	Sitting on hind quarters
Barking*	Short loud bark
Whining*	Long, high-pitched vocalization

occurrences were summed for each behavior. In the one-zero sampling, we recorded which behavior occurred in the first 30 s, then in the second, third, fourth, fifth, and sixth 30 s interval. All points of a behavior occurred in all six intervals were summed to calculate the total point for each behavior in the entire 3 min (maximum 6 points), and these total points were used in the further analysis. After the 3 min observations, juvenile foxes were immediately handled for ear-tagging, checking sex and weighing, and released. Most trappings and observations were done in early and mid-July and we therefore assumed their behavior to be relatively little affected by their size and age.

Statistical analyses

All behavior variables (Table 1) from the first human approach test and the first juvenile trapping were standardized by centering to mean zero and scaling to unit variance. All statistical analyses were conducted in R version 3.1.2. We used a principal component analysis (PCA) commonly used in personality research to determine if individuals' behaviors were correlated into distinct personality traits. To capture most of the variance of the original variables, PCA transforms a set of possibly correlated variables into a smaller set of uncorrelated variables, or components that may be interpreted as a behaviorally significant trait. PCA then allocates a score on each component to each individual, thus allowing us to compare individual scores on the certain behavior trait. We used the *principal* routine in the *psych* package in R. We determined the number of components with Horn's parallel analysis using *fa.parallel* routine in the *psych* package to produce 1000 random datasets and calculate their eigenvalues. The original variables were defined by their loading on the new components indicating the correlation strength (from -1 to $+1$) between the component and each original behavior variable. From the loadings, we calculated individual scores as below for each component using the equation

$$\text{Score} = \sum_{i=1}^n t_i L_i$$

where n is the number of behaviors in the PCA, t_i is the frequency or scaled time spent on behavior i and L_i is the loading of behavior i on the component. We used only salient behaviors ($|\text{loading}| > 0.4$ in magnitude) for a clearer interpretation. We then standardized scores.

From individuals tested for multiple times, repeatability of each individual's standardized scores was calculated using the intra-class correlation coefficient (r).

$$r = s^2_A / (s^2 + s^2_A)^2$$

where s^2_A is the among-individual variance and s^2 is the within-individual variance. Hence r represents the proportion of the variance that is due to the differences among individuals ($r = 1$ indicates perfect repeatability, and $r = 0$ indicates random behavior between tests). We also calculated the 95% confidence intervals for each individual's repeatability to test significant deviation from 0 using the likelihood surface.

Before investigating correlations between individual scores for each component retained by the PCA and fitness-related factors, we firstly compared personality scores between male and female adults, and between adults living as a pair and adults living in a complex family group (i.e., more than two adults living in the same den) using the function *t.test* in R. To compare different dens, we then calculated average parent scores by averaging individual scores of adults by den. However, in 5 (out of 10) dens where only one individual adult was tested, we used the individual score as a parent score for the den. Similarly, average juvenile den-level scores were calculated by averaging all individual scores by litter.

We used linear mixed-effect models using the function *lmer* in the package *lme4* in R to test if the behavioral traits were related to juvenile mortality rate and to juvenile condition index. We used the following variables as fixed effects in both mortality and condition models: (a) parent personality scores, (b) juvenile scores for three behavioral traits averaged by den respectively. Secondly, we tested each of the average juvenile behavior scores with respect to average parent personality scores as fixed effects. Also, we tested if average juvenile condition index affected the den-level mortality rate using the linear mixed-effect model. Lastly, we tested the relationship between parent and juvenile behavior by linking average parent scores with average juvenile behavior scores using *lmer*. We used area (Vindelfjällen or Helags) as a random effect in all models. We obtained p values by likelihood ratio test of the full model with the variable in question compared to the model without the variable in question. The significance level was set as below 0.05.

Results

Individual behavioral differences in adult and juvenile arctic foxes

To answer the first question of if there was consistent behavior variation in the studied population, we tested adult behaviors through the human approach test and two behavioral components were retained by the PCA ($n = 17$, Table 2). One component was related to vigilance including early barking latency, more barking, watching observer, watching sides, and standing behavior. The second component was related to bold behaviors and associated with late hiding latency, lack of hiding and of

Table 2 Loadings from the principal component analysis (PCA) on arctic fox behaviors through the adult human approach test and 3-min behavior observation of juveniles in a trap (juvenile trap behavior). *Italic numbers represent salient behaviors used for calculating individual personality scores*

Test	Adult human approach		Juvenile trap behavior observation			
	Vigilance	Boldness	Behaviors	Investigating	Passive	Escaping
Barking latency	<i>0.84</i>	-0.16	Lying down	-0.39	<i>0.5</i>	-0.12
Hiding latency	-0.41	-0.75	Moving around	<i>0.79</i>	-0.02	0.26
Relaxing latency	0.14	0.21	Digging	-0.02	-0.24	<i>0.5</i>
Warning bark	<i>0.94</i>	-0.11	Scratching side	<i>0.76</i>	0.00	-0.08
Watching observer	<i>0.85</i>	0.12	Biting trap	0.02	-0.63	0.22
Hiding	-0.28	-0.79	Standing still	0.12	<i>0.72</i>	-0.11
Watching side	<i>0.59</i>	0.3	Sniffing	<i>0.45</i>	0.38	0.3
Fleeing	0.07	-0.75	Pushing	0.17	-0.08	<i>0.72</i>
Moving around	-0.06	0.35	Eating	-0.1	0.05	-0.41
Lying down	-0.26	<i>0.41</i>	Sitting still	-0.04	0.28	0.24
Standing	<i>0.57</i>	-0.04	Barking/whining	0.49	-0.22	-0.55
Sitting	-0.05	0.3				
Proportion variance explained	0.28	0.19		0.17	0.14	0.14
Cumulative variance explained	0.28	0.47		0.17	0.31	0.44

fleeing, and more lying down behavior. These two components both showed significant repeatabilities ($n = 10$, $r = 0.72$, 95% Confidence Intervals [CI] = 0.32, 0.89, and $r = 0.66$, 95% CI = 0.19, 0.86 for the first and second component respectively) and explained 44% of the variance. We named the first component as “vigilance,” and the second as “boldness.” There was no difference in any personality scores between female ($n = 10$) and male adults ($n = 4$; $t = -0.90$, $df = 4.21$, $p = 0.42$ for vigilance; $t = -0.79$, $df = 10.79$, $p = 0.45$ for boldness), and between individuals living as a pair ($n = 4$) and individuals forming a complex group ($n = 4$) with more than two adults living in the same den ($t = 0.12$, $df = 13.27$, $p = 0.91$ for boldness, $t = -1.61$, $df = 15.00$, $p = 0.13$ for vigilance).

The PCA for individual juvenile foxes retained three behavioral components ($n = 104$, Table 2). The first component involved moving around, scratching side, and sniffing which we considered to be associated with investigating behavior. The second trait contained lying down, standing still, and less biting behavior which might calibrate passiveness in a stressful situation. The last trait included digging, pushing, lack of eating and barking/whining and was related to how much time an individual spent in trying to escape or trying something else like eating or barking/whining in the other end of the trait. When tested from retrapped juveniles ($n = 34$), these three components showed no significant repeatability ($r = 0.39$, 95% CI = -0.004, 0.62 in investigating behavior, $r = 0.24$, 95% CI = -0.23, 0.51 in passive behavior, $r = 0.37$, 95% CI = -0.043, 0.60 in escaping behavior). Generally speaking, 73% of the retrapped juveniles

showed decreased investigating and escaping behavior, and 60% showed an increased passive behavior during the second trapping.

Observations on predators, juvenile mortality rate and physical condition

In 2015, the juvenile survival was extremely low through the summer and autumn. Of 152 juveniles at 19 dens monitored for mortality, only 78 juveniles survived to the end of July or early August (Appendix Table 3). Further camera trappings through the late summer and autumn indicated that only very few individuals survived to dispersal (data not present). Not a single juvenile fox was found alive subsequent years despite intensive inventories in Sweden and Norway. We found, however, a considerable variation in weekly mortality rate between litters from 0 to 27% (Appendix Table 3). Average mortality rate was 13% (16% in Vindelfjällen and 12% in Helags) with no significant difference between the two areas ($t_{18} = 0.7$, $p = 0.49$). Furthermore, we observed numerous interactions between arctic foxes and their predators during the summer ($n = 32$); mostly golden eagles ($n = 25$) and some wolverines ($n = 4$; Appendix Table 3). We directly observed predators scanning or attacking arctic fox dens in 9 out of the 30 dens and found 5 freshly killed foxes at 3 out of the 10 dens in Vindelfjällen. Condition indices of juveniles also varied between litters ranging from 0.92 to 1.37 with the average of 1.08 but remained similar within litter over the summer despite the high mortality rate, which might indicate predation was the main cause of the high mortality (Appendix Table 3).

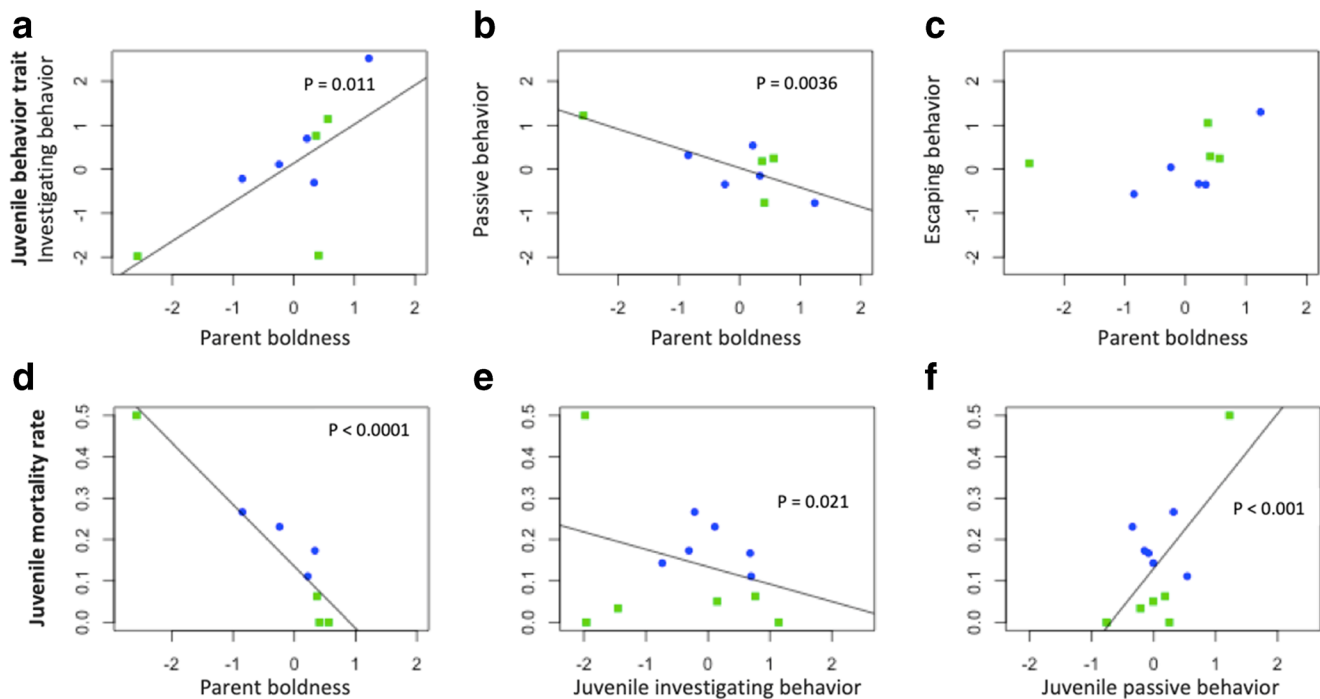


Fig. 2 The relationship between standardized scores of juvenile behaviors tested under stress in a trap (i.e., investigating, passive, escaping) and standardized parent boldness scores tested through their reactions toward human observers (a, b, c). Juvenile mortality rate in

relation to standardized parent boldness score (d), and to standardized juvenile investigating and passive behavior score (e, f). Blue circles represent Vindelfjällen and green boxes represent Helags data averaged by litter

The relationship between adult and juvenile behavioral traits

To answer our second question if adult and their juvenile behavior were correlated, we further investigated the relationship between adult and juvenile behavioral traits in 9 litters. We found that adult boldness was related to juvenile investigating scores ($\chi^2(1) = 6.48$, $p = 0.011$; Fig. 2a), raising it by $0.82 \text{ score} \pm \text{SD } 0.27$, whereas adult vigilance did not show any relationships to juvenile investigating scores ($\chi^2(1) = 3.54$, $p = 0.060$). Adult boldness also negatively influenced passive scores of their juveniles ($\chi^2(1) = 8.47$, $p = 0.0036$; Fig. 2b), lowering the average score by $0.46 \pm \text{SD } 0.12$. However, we did not find any significant relations between juvenile escaping scores and both adult personality traits ($\chi^2(1) = 2.14$, $p = 0.14$ for boldness, Fig. 2c; $\chi^2(1) = 0.91$, $p = 0.34$ for vigilance).

The relationships between adult and juvenile behavior, juvenile mortality rate, and physical condition

Lastly, we have investigated how adult and juvenile behavior were related to fitness components, i.e. juvenile mortality and physical condition. We first investigated the relationship between the average parent scores from each personality trait (i.e., boldness, vigilance) and their juvenile mortality rate in

8 litters. Parent boldness strongly affected juvenile mortality rate ($\chi^2(1) = 21.23$, $p < 0.0001$), lowering it by $15.6\% \pm \text{SD } 1.3$ (Fig. 2d), while parental vigilance was not related to mortality rate ($\chi^2(1) = 0.78$, $p = 0.38$). Secondly, we tested the relationships between juvenile behavior and mortality in 12 litters. We found two of three juvenile behavioral traits that were significantly related to juvenile mortality rate. Juvenile investigating scores were negatively related to their mortality rate ($\chi^2(1) = 5.35$, $p = 0.021$; Fig. 2e) lowering the mortality rate by about $7.5\% \pm \text{SD } 2.2$, and juvenile passive scores positively affected juvenile mortality rate ($\chi^2(1) = 11.32$, $p = 0.00077$; Fig. 2f) raising it by about $20\% \pm \text{SD } 4.1$. Escaping scores of juveniles did not show any relation to their mortality rate ($\chi^2(1) = 1.11$, $p = 0.29$). Condition index averaged by litter ($n = 20$) seemed to show a weak negative relation to mortality rate but was not statistically significant ($\chi^2(1) = 3.79$, $p = 0.051$).

We then investigated if parent or juvenile behavior was related to juvenile condition index in 9 litters. For parent personalities (i.e., boldness, vigilance) and juvenile condition index, there were no significance relationships between them ($\chi^2(1) = 1.53$, $p = 0.21$ for boldness score, $\chi^2(1) = 0.0082$, $p = 0.93$ for vigilance score). We also found no significant relationship between juvenile condition index and scores of three juvenile behavioral traits ($\chi^2(1) = 0.0006$, $p = 0.98$ for investigating score, $\chi^2(1) = 0.0008$, $p = 0.98$, for passive score, $\chi^2(1) = 0.11$, $p = 0.74$ for escaping score).

Discussion

As a summary of our questions and the results, the conceptual relationships between adult personality, juvenile behavior, physical condition, and their relationship with mortality rate are shown in Fig. 1. We found a major pattern (thick lines in Fig. 1) where a parent personality trait (boldness) was negatively related to juvenile mortality rate and juvenile passiveness, and positively with juvenile investigating behavior. In turn, more passive and less investigating juveniles had higher mortality rate.

Individual variation in personality and behavior traits in adult and juvenile arctic foxes

We found significant variability in how adult foxes reacted to a risky stimulus measured through the human approach test. We detected two uncorrelated personality traits, vigilance and boldness, related to their risk perception toward a potential predator (i.e., approaching human observer). Interestingly, we found no difference between sexes, or between different types of family group in all behavior traits, indicating that these are personality traits independent of the environment. We also found that individual juvenile foxes reacted differently to a stressful situation in a trap. Through this, we extracted three behavioral traits (i.e., investigating, passive, escaping) demonstrating how they reacted to stress and dealt with problems that they faced, which might show a spectrum in passiveness of the individual juveniles (Koolhaas et al. 1999).

We found strong repeatability in adult behavior in how they guarded their juveniles, while the repeatability of juvenile behavior traits was substantially lower. None of the behavior traits for trapped juvenile foxes were as strongly repeatable as those of adult foxes. Juveniles that were retrapped tended to behave differently compared to their first trapping and likely were habituated to the trap, showing less stress-related behavior. Some juveniles became extremely habituated and were trapped many times (up to 30 times) with short intervals. However, the rate of such process differed between individuals which might be due to individual differences in behavioral plasticity. Other studies have also reported behavioral plasticity of juvenile arctic foxes in that their behavior traits were not repeatable through time and their ontogeny (Nilsson 2013; Grocutt 2015). Although adults and juveniles were tested using different experiments, the difference in repeatability between adults and juveniles is of particular interest which deserves further studies. For a developmental perspective, juveniles might undergo dramatic developmental changes and could be expected to show less repeatable behavior than adults (Bell et al. 2009). Also for an evolutionary point of view, the difference in repeatability between adults and juveniles might reflect selection pressures on phenotypic variance since the

variance would be reduced if there is directional or stabilizing selection (Bell et al. 2009).

The intensified mortality process and the roles of adult personality

The summer of 2015 provided a unique situation with a lemming peak in the winter followed by an early summer lemming crash (The Swedish Arctic Fox Project 2015). There was the highest number of arctic fox litters in Sweden since the twentieth century (in total 88 litters) with large litter sizes. However, the survival of juveniles during the summer was extremely low and only a few juveniles from a single litter survived their first summer. The weekly mortality rate was much higher (13%; 12% in Helags, 16% in Vindelfjällen) than previously reported mortality rates from the same Helags population in a lemming decrease phase (Meijer et al. 2011, 2013).

Since a supplementary feeding program was implemented in 2001 and has been proved to lower mortality rate (Angerbjörn et al. 2013), this extreme mortality process seemed to be predation-induced. During our summer monitoring, we have also observed that juveniles could use a supplementary feeder located about a hundred meters away from the den, but parents also brought dog pellets to the juveniles. The average condition index of juveniles was 1.08, with a low difference between litters and within litter (Appendix Table 3). The average condition index of all juveniles was higher than the average condition indices in previous years with only access to natural food sources (Tannerfeldt et al. 1994). We found that physical conditions of juveniles were not related to their mortality rate and did not fluctuate within litter over the summer suggesting that they did not starve to death (Appendix Table 3). Many predator species in the arctic environment depends heavily on the lemming cycles (Ims and Fuglei 2005). The early summer lemming crash could thus intensify the intraguild competition for a limited prey resource and even result in intraguild predation on arctic fox juveniles when top predators would switch their prey base from lemmings or other game species to juvenile arctic foxes (Tjernberg 1983; Gilg et al. 2003; Meijer et al. 2011; Erlandsson et al. 2017).

In this strong mortality process, we found that parent boldness showed a strong negative relation to juvenile mortality rate. Stronger selection pressures could thus favor one end of the spectrum of a personality trait in such context when there was higher predation risk. Selection favoring bold individuals has also been seen in bighorn sheep (*Ovis canadensis*) during years of high predation while there was no selection in years with low predation (Réale and Festa-Bianchet 2003). In a study of European mink where captive-bred animals were released in the wild, bold animals survived better in one year as a response to high predation but shy animals survived

another year in connection with starvation (Haage et al. 2017). In swift foxes (*Vulpes velox*), in contrast, bold individuals showed increased mortality as they were more attracted by a novel risk such as road and got road-killed (Bremner-Harrison et al. 2004). This demonstrated the importance of the local conditions and of identifying the main cause of mortality (e.g., predation, starvation, novel risk) in the ecosystem. This illustrates that fluctuating environmental conditions could switch selection pressures for different personality types (Bremner-Harrison et al. 2004; Cole and Quinn 2014). In our study, bolder parents might be better at dealing with stress induced by perceived risks and be more efficient in guarding their offspring. Behavioral differences in antipredator strategies between parents have also been suggested to be an important for juvenile survival in the arctic fox (Meijer et al. 2011; Erlandsson et al. 2017). However, bolder parents, for example, might have higher mortality of themselves despite higher offspring survival, as they might be more likely to be depredated by predators such as eagles or wolverines. Future studies including different environmental conditions would be needed to fully understand trade-offs between different behavior strategies and the ecological processes undergoing in the system.

The effect of juvenile behavior traits on mortality rate

Higher scores on the passive behavioral trait for juvenile arctic foxes were related to an increase in the mortality rate whereas high scores on the investigating behavioral trait were associated with a decrease in their mortality rate. These behavioral traits seemed to be related to low risk responsiveness along a passive–activeness spectrum indicating whether individuals are actively exploring the risk and trying to escape or not during stressful or risky situations. Previous studies have suggested that behavioral traits which are related to individual's perception toward risks result in mortality according to environmental contexts (Bremner-Harrison et al. 2004; Smith and Blumstein 2008; Norén and Angerbjörn 2013; Erlandsson et al. 2017; Haage et al. 2017). Through the habituation in juvenile behaviors in a trap (passiveness increased in the second trapping compared to the first trapping), it is also likely that this behavioral trait captured the low sensitivity of individuals toward novel and stressful stimuli. In this sense, more passive individuals might have a lowered stress response toward stress or risk making them susceptible to predation. This might be a possible mechanism explaining higher juvenile mortality rate in more passive and less investigating juveniles. However, plausible mechanisms behind this mortality pattern together with ontogenetic factors for juvenile behavior need to be investigated further to fully understand this phenomenon.

The influence of variation in adult personality on juvenile behavior traits

Bold adult arctic foxes had juveniles with lower mortality rates and which were behaviorally less passive and more investigative. Thus, there might be an indirect effect of adult personality on juvenile mortality mediated through juvenile behaviors. Elucidating the connections between adult personality, juvenile behavior and mortality rate would be important for future study. Together with the environmental factors, genetic components for such individual difference as suggested in other species (Dochtermann et al. 2015) should be taken into account to fully understand inter-twined connections between behavior of parents and offspring and the fitness-related processes.

Ecological implications

Individual variation within a population, such as variation in personality, can affect ecological interactions, population stability, and ecological dynamics (Bolnick et al. 2011). Especially in changing environments, we need to consider such individual variation and interactions with changing factors to better predict dynamics of a population. The cyclic environments in the northern ecosystems are particularly interesting to study with regard to such personality-mediated dynamics.

Chitty (1996) suggested that individual variation in intrinsic factors could affect life history variables and thereby population dynamics. Such factors could be differences in behavior, physiology or genotype that are sensitive to mortality. We suggest that the connection between variation in adult personality and juvenile mortality in arctic foxes could be seen as such an example. However, it remains unclear if this would affect the population dynamics or cycles.

The summer of 2015 in the Swedish mountains provided an interesting natural experiment of these dynamics. Juvenile mortality was much higher compared to years with plentiful prey source. If there is selection on personality in the arctic fox population and the selection pressure varies according to different phases of the lemming cycle, it could explain the variation in personality within the arctic fox population. In addition, possible trade-offs should be taken into account in explaining the maintenance of such variation, since bold individuals might trade off their own survival for higher reproductive success, and vice versa for shy individuals (Smith and Blumstein 2008). It has been suggested that variation in personality traits is maintained through differential selection pressures in relation to fluctuating environmental factors together with different competition intensity or predation risks (Réale et al. 2000; Dingemanse et al. 2004; Haage et al. 2017). Our results suggest a mechanism driving fluctuations in the

frequency of different personality traits in a species living under fluctuating environments.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Ethical approval Trapping and handling procedures were carried out following the Swedish law and the Swedish Board of Agriculture (Jordbruksverket) and the ethical board (Umeå djurförsöksetiska nämnd, ethical permits: A130-07, A131-07, A36-11, A18-14 and A19-14). Considering the conservation status of the Swedish arctic fox population, trapping had to be permitted by the Swedish Environmental Protection Agency (Naturvårdsverket, permit: 412-7784-07 NV, NV-01959-14).

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

Appendix

Table 3 Arctic fox behavior, physical condition, reproduction, and mortality data used in the study

Area	Den	Visit	#Adult	Minimum litter size	Condition Index ± stdev	Weekly mortality	Human approach n* (repeat†)	Juvenile trap behavior n (repeat)	Method	Species (n)	Predators	Comments on interactions
Vindel-fjällen	A4b	7–9 Jul	2	7	1.062	0.143	-	-	-	-	-	-
		21–22 Jul	2	6	0.916±0.044	-	-	4 (1)	one-zero	Probably eagle (1)	Found one cub predated	
	A5	8–9 Jul	1	5	-	0	-	-	-	-	-	-
		19–21 Jul	2	10	1.080	-	-	-	-	-	-	-
	A16	7–14 Jul	2	12	1.063±0.067	-	-	-	1	one-zero	-	-
		7–13 Jul	3	13	1.065±0.066	0.173	3 (2)	12 (7)	one-zero	-	-	-
	R11‡	3–6 Aug	0	4	-	-	-	-	-	Golden eagle (2), eagle (3)	3 eagles flying app. 2km away from the den, a golden eagle flying right above the den scanning 2 times (no cubs out)	
	R3‡	5–8 Jul	2	14	0.988±0.080	0.167	-	10 (2)	one-zero	-	-	-
		21–24 Jul	1	5	-	-	-	2	one-zero	-	-	-
	R5‡	7–9 Aug	0	2	-	-	-	-	-	-	-	-
		9–10 Jul	3	3	1.051±0.103	0.231	3 (0)	3	one-zero	Golden eagle (1)	A golden eagle flying by the den	
	R5‡	17–21 Jul	3	26	1.026±0.092	-	(2)	5 (4)	one-zero	Unknown	One untagged white adult found freshly killed and predated	
		1–3 Aug	1	8	-	-	-	-	-	Golden eagle (1)	Spotted eagle 2km away before the arrival and then found one cub predated and the left carcass being eaten by siblings	
	T13‡	4–7 Jul	1	15	1.042±0.058	0.267	1 (1)	7 (2)	one-zero	-	-	-
		13–15 Jul	1	9	-	-	-	-	-	Golden eagle(1)	Directly observed one eagle hunting a cub but dropping the cub from the sky when adult barked and ran toward it	
T8‡	24–26 Jul	1	3	1.066	-	(1)	(2)	-	unknown	Found one predated tagged cub 1.5 km from the den (23 July)		
	10–13 Jul	2	12	1.164±0.094	0.111	2 (1F)	6 (2)	one-zero	-	-	-	
V1	26–28 Jul	2	8	-	-	(2)	-	-	-	-	-	
	23–27 Jul	2	12	1.084±0.049	-	1	4 (1)	one-zero	-	-	-	
V3	19–23 Jul	3	11	1.133±0.075	-	-	6 (2)	one-zero	-	-	-	
Hulke	11–12 Jul	3	7	1.252	-	-	5	one-zero	-	-	-	
Latsdalen	14 Jul	3	7	1.071	-	-	1	one-zero	-	-	-	
ZZ009§	23–24 Jul	1	5	1.173±0.162	0.022	-	-	-	-	-	-	
ZZ013	11–12 Jul	2	4	1.138±0.098	0	2 (1M)	4 (1)	continuous	-	-	-	
ZZ015	22–24 Jul	2	4	-	-	(1F)	-	-	-	-	-	
ZZ015	12–13 Jul	2	4	1.154±0.079	0.167	-	-	-	-	-	-	
ZZ015	1–2 Aug	2	2	-	-	-	-	-	-	-	-	
ZZ016	24–25 Jul	5	3	-	-	2	-	-	Golden eagles (4), white-tailed eagle (1)	1 and 2 golden eagles (8 Jul and 24 Jul), a white tailed eagle flying by/over the den. A golden eagle landing on the den (25 Jul).		
ZZ018	11–12 Jul	3	8	1.074±0.033	0.063	1	5 (1)	continuous	-	-	-	
ZZ018	25–27 Jul	3	7	-	-	-	-	-	-	-	-	
ZZ019	4–5 Jul	3	12	1.204±0.148	0.050	-	7 (1)	continuous	Golden eagle (1)	A golden eagle landing on the den, adults giving alarm calls hiding.		
ZZ019	2–4 Aug	3	9	1.276±0.103	-	-	-	-	Wolverine (1), golden eagle (1)	A wolverine digging the den, adult barking, and a golden eagle flying over the den, adult giving alarm calls		
Helags	ZZ020	10–11 Jul	2	11	1.073±0.131	0.100	-	1	one-zero	-	-	-
	ZZ020	24–25 Jul	2	8	1.016±0.220	-	-	-	-	-	-	-
	ZZ023	14–16 Jul	3	7	1.140±0.118	-	-	5 (5)	continuous	-	-	-
	ZZ024§	11–12 Jul	2	6	0.917	0.143	-	-	-	Eagle (8)	From camera trap, eagles landing on the den 8 times (4–25 Jul)	
	ZZ029	11–12 Jul	2	6	1.365±0.080	-	-	5 (2)	one-zero	-	-	-
	ZZ030	21–22 Jul	1	8	1.092±0.111	0.200	-	-	-	-	-	-
	ZZ030	30 Jul?	1	6	-	-	-	-	-	-	-	-
	ZZ035	15–16 Jul	2	3	0.966±0.168	-	-	2	one-zero	-	-	-
	ZZ042	8–9 Jul	2	10	1.168±0.050	0.033	-	2	continuous	-	-	-
	ZZ064§	12–13 Jul	2	7	0.979±0.070	0.100	-	-	-	-	-	-
ZZ066§	13–14 Jul	2	7	1.037±0.189	0.143	-	-	-	Eagle (2)	From camera trap, eagles landing on the den two times later in the summer (22 Aug, 3 Sep)		
ZZ080	12–13 Jul	2	3	1.152±0.038	0.000	1	2 (1)	continuous	Wolverines (3)	3 wolverines coming to the den and leaving when fieldworker trapped a cub.		
ZZ090	30–31 Jul	0	4	-	-	-	-	-	-	-	-	
ZZ090	14–15 Jul	2	4	-	0.500	1	1	continuous	-	-	-	
ZZ090	22–23 Jul	2	2	-	-	-	-	-	-	-	-	
ZZ096	20–21 Jul	1	4	1.173±0.096	NA	-	4 (1)	continuous	-	-	-	
total	30 dens		58 indiv	234 indiv	28 dens	19 dens	17 indiv (10)	104 indiv (35)				

*The number of individuals tested or observed, † the number of repeated individuals, F means female while M means male, ‡ bold underlined dens includes individual-level survival data through observation, re-trapping, and/or camera trapping later in the summer (late July or early August), § bold italic dens were scanned through camera traps for the longer period (over the whole summer) to monitor mortality

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