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ORIGINAL ARTICLE

Prey availability influences the effect of boldness on reproductive success in a mammalian predator

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Abstract

Boldness is an important trait in wild populations, and among-individual differences can link to individual fitness. The strength and direction of relationships between behavioral and life-history traits may however vary according to environmental conditions, where fluctuating selection acting on behavioral traits contributes to the maintenance of personality differences. We explored sources of variation in Arctic fox (*Vulpes lagopus*) boldness and investigated how temporal variation in the abundance of a main prey (lemmings) influences the relationship between fox boldness and reproductive success. We measured the behavioral reaction of individuals when escaping after handling, as an indicator of their boldness. We obtained 70 measurements from 42 individuals during two years of low lemming abundance and 2 years of high lemming abundance and assessed fox litter size as an indicator of reproductive success. First, individual characteristics (age, sex, mass) did not affect Arctic fox boldness, while individual identity generated variation in boldness. Next, we found that during years of low lemming density, individuals behaving boldly had more pups than those behaving less boldly, suggesting boldness may provide an advantage when lemmings are scarce by increasing hunting success or allowing access to alternative resources. However, all individuals tended to show high levels of boldness when lemming density was high, and all produced large litters. Temporal variation in the abundance of a main prey might therefore influence the relation between boldness and reproductive success of a predator, and if individuals consistently differ in their level of boldness, fluctuating selection could contribute to the maintenance of personality.

Significance statement

Effects of boldness on Arctic fox reproductive success: lemming abundance matters! When lemmings are scarce, foxes showing bold behavior have more pups than foxes showing less bold behavior. This highlights that under low prey availability, boldness may bring short-term benefits to predators, potentially because it allows to acquire more food. When lemmings are abundant, however, all foxes produce as many pups. This shows that environmental conditions such as prey abundance can influence the relation between behavior and reproductive success in a predator. Studying the context-dependency of relationships between behavior and reproductive success is critical to better understand ecological and evolutionary consequences of environmental change.

Keywords Arctic fox · Boldness · Litter size · Personality · Predation · Resource abundance

Introduction

Individuals within populations of many species differ consistently in behavioral traits such as boldness (i.e., an individual's willingness to take risks, measured on a bold–shy continuum), both over time and across contexts (Réale et al. 2007, 2009; Carter et al. 2013). Consistent among-individual differences, or personality, have also been highlighted for other behavioral traits such as exploration of novel environments, activity, aggressiveness, and sociality (Réale

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et al. 2007). Those behavioral traits may covary and form a behavioral syndrome (Sih et al. 2004). Personality traits have important evolutionary implications as they can explain fitness variation (Dingemanse and Réale 2005; Smith and Blumstein 2008; Réale et al. 2009). Bolder and more aggressive individuals usually grow faster and are more fecund since they tend to maximize foraging and reproduction opportunities (Biro and Stamps 2008; Smith and Blumstein 2008). For example, bolder female grey seals (*Halichoerus grypus*) produce heavier pups than shyer ones (Bubac et al. 2018). However, boldness could also be associated with a reduction in lifespan, potentially because bolder individuals engage in more risky situations that increase mortality risk (e.g., through predation), but also because boldness incurs physiological costs such as higher metabolic rates and thus greater costs of living (Wolf et al. 2007; Smith and Blumstein 2008; Réale et al. 2010; but see Moiron et al. 2020). Individuals of different behavioral types therefore resolve life-history trade-offs in alternative ways, favoring either current or future reproduction but reaching an equivalent lifetime reproductive success, which should contribute to maintain personality differences in populations (Wolf et al. 2007; Réale et al. 2010; but see Montiglio et al. 2018).

Trade-offs between current and future reproduction may thus lead to consistent among-individual differences in personality traits, but they can also lead to within-individual variation in behavior (e.g., through phenotypic plasticity). First, residual reproductive value varies with individual traits such as age and body condition. As younger individuals have more reproductive opportunities ahead of them, they should act less boldly compared to older individuals that should favor current reproduction (Dammhahn 2012; Bubac et al. 2018). Similarly, individuals in good body condition should be less bold as they have a greater potential for future reproduction, compared to individuals in poor condition (Moran et al. 2021). Therefore, individuals may become bolder as they age, and boldness could vary throughout an individual's life according to its body condition (Dammhahn 2012; Moran et al. 2021). Females and males may also differ in their expression of some behavioral traits and in their degree of behavioral consistency, and these differences may result from sexual selection where selection pressures differ between males and females (Schuett et al. 2010).

The life-history trade-off hypothesis thus predicts that bolder, more aggressive individuals will favor current reproduction and live shorter lives. However, empirical studies show that the strength and direction of relationships between behavioral and life-history traits can vary. For example, Bridger et al. (2015) found that in male hermit crabs (*Pagurus bernhardus*), shy individuals were more fecund than bold ones. Moreover, in female great tits (*Parus major*), the relationship between exploration and reproductive success varied according to food availability (Dingemanse et al. 2004). In fact, fluctuating environments, especially fluctuating food resources, may influence the strength and direction of relationships between behavioral and life-history traits, where bolder individuals are favored over shyer ones, or *vice versa*, depending on environmental conditions. For example, in Siberian chipmunks (*Tamias sibiricus*), the boldest individuals have the greatest annual reproductive success during years of low food availability, but the opposite is true when food is abundant (Le Cœur et al., 2015). Furthermore, female wild boars (*Sus scrofa*) that are the least aggressive and that show the lowest exploratory tendencies have the greatest reproductive success, but only when their main food is abundant (Vetter et al. 2016). In female American red squirrels (*Tamiasciurus hudsonicus*), the effects of activity level on offspring growth rate, and of aggressiveness on offspring survival, vary in magnitude and direction according to food abundance (Boon et al. 2007). Fluctuating selection acting on behavioral traits is another potential mechanism explaining the maintenance of personality differences in wild animal populations (Dingemanse et al. 2004; Wolf and Weissing 2010; Le Cœur et al., 2015; Mouchet et al. 2021), where various ecological variables influence associations between behavior and life-history traits (Smith and Blumstein 2008; Adriaenssens and Johnsson 2009; Montiglio et al. 2018). Still, only a handful of studies have assessed such context-dependent relationships, using as model species insectivorous birds (Dingemanse et al. 2004; Quinn et al. 2009), rodents (Boon et al. 2007; Bergeron et al. 2013; Le Cœur et al., 2015) and other herbivores (Vetter et al. 2016). Studying those relationships is critical to better understand how personality differences may be maintained in animal populations, and more broadly to inform on ecological and evolutionary consequences of environmental change.

In this study, we assessed how the boldness of a predator predicts its reproductive success across variable prey abundances. We studied the Arctic fox (*Vulpes lagopus*), a predator showing consistent among-individual differences in boldness within years (Choi et al. 2019) and subjected to cyclic variation in the abundance of its main prey (lemmings, *Lemmus* and *Dicrostonyx* spp.) across most of its circumpolar distribution (Audet et al. 2002; Angerbjörn et al. 2004). While it is clear that the abundance of lemmings influences Arctic fox probability to reproduce (Chevallier et al. 2020; Juhasz et al. 2020) and litter size (Tannerfeldt and Angerbjörn 1998), the role of boldness in mediating this relationship is unknown. The general aim of this study was thus to evaluate whether prey abundance affects the relationship between boldness and reproductive success in the Arctic fox. The fitness of predators being highly dependent on prey availability (Salamolard et al. 2000; Terraube et al. 2015), their reproductive success under low prey availability should depend on their capacity to obtain valuable food resources. Boldness, which might relate to hunting strategies (Patrick et al. 2014; Chang et al. 2017), could therefore be beneficial under low prey availability. However, as boldness incurs costs, acting boldly may be less beneficial when prey are abundant.

We estimated the litter size and boldness of Arctic fox parents by counting their pups at dens and observing their escape behavior after handling. We did so during 2 years of low lemming abundance and 2 years of high lemming abundance in Nunavut, Canada. We first explored sources of variation in Arctic fox boldness, by evaluating how individual characteristics (age, sex, and mass) and consistent among-individual differences influenced fox behavioral reaction to a risky situation, that is the handling environment from which they were escaping. Second, we tested the hypothesis that the effect of boldness on litter size depends on lemming density. We predicted that (1) when lemmings are scarce, individuals behaving boldly would have larger litter sizes than individuals behaving less boldly, since bold individuals may be more efficient at acquiring resources, but (2) when lemmings are abundant, individuals behaving boldly would have similar or smaller litter sizes as those behaving less boldly, since shy individuals may be just as efficient at acquiring resources in such conditions and behaving boldly may incur additional costs.

Methods

Study system

We conducted fieldwork from 2016 to 2019 in the southwest plain of Bylot Island (73° N, 80° W), in Sirmilik National Park of Canada, Nunavut, where the Arctic fox is the main terrestrial predator. At Bylot Island, fox probability of reproduction is highly dependent on the abundance of brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*), and on the access to a large greater snow goose (*Anser caerulescens atlanticus*) colony (Chevallier et al. 2020; Juhasz et al. 2020). Lemmings follow a 3–4-year cycle in abundance, but fluctuations are much stronger for brown lemmings, the most abundant species (from < 1 to 10 individual/ha for brown lemmings and always < 1 individual/ha for collared lemmings; Gruyer et al. 2008; Gauthier et al. 2013; Fauteux et al. 2015). The snow goose colony (> 20,000 nesting pairs, Bêty et al. 2001) is restricted to a ca. 60 km^2 area in the southern portion of the study area. The goose colony provides an alternative food resource during summer, and foxes may take and cache goose eggs for consumption during the rest of the year (Careau et al. 2008). In years of low lemming abundance, foxes with access to the snow goose colony have a higher probability of reproducing than those without access (Giroux et al. 2012; Chevallier et al. 2020). The greater snow goose is a relatively large bird, with a wingspan of ca. 1.5 m and weighing up to 3.5 kg. Small Arctic foxes (ca. 3 kg) that attempt to take goose eggs from nesting pairs are faced with aggressive defense behaviors from both parents (Bêty et al. 2002).

Fox captures and behavioral measurements

We captured Arctic foxes using Tomahawk cage traps #205 (Tomahawk Live Trap Company) or Softcatch #1 padded leg-hold traps (Oneida Victor Inc. Ltd.). At each capture, we marked individuals with 4 colored ear tags allowing identification at a distance, weighed them to the nearest g, determined their sex from genitalia characteristics, and assessed whether females were lactating. We also took pictures of full dentition to estimate age from visual analysis of tooth wear (Chevallier et al. 2017). Foxes were sometimes anesthetized if they were too aggressive to be handled. We used a combination of medetomidine (0.05 ml/kg) and ketamine (0.025 ml/kg), and then atipamezole (0.05 ml/kg) as a reversal agent, before releasing foxes at the capture site.

Different measurements may be used to assess the boldness of wild animals, such as the latency to emerge from a refuge, flight initiation distance, or reaction towards a novel object (Réale et al. 2007; Carter et al. 2013). We measured foxes' level of boldness by assessing their reaction when released after the manipulations described above. Escape behavior after handling has also been used to evaluate boldness in other species (Jornod and Roche 2015; DeRango et al. 2019). More specifically, once released, a fox escapes the danger represented by the observers handling them by running away, and its behavior should reflect its willingness to take risk. At some point, the fox stops and turns its body and head to look back at the observers (hereafter referred as a turnaround), potentially to re-assess the danger. At each release, we thus measured to the nearest meter the distance at first turnaround, using a telemeter or counting 1-m steps between the release point and the location at which the fox first stopped and looked back at the observers. We also noted the general pace of the fox when escaping, which was scored as slow, intermediate, and fast pace. As much as possible, we released individuals in flat areas free of obstacles. Video examples of releases are included as supplementary material to demonstrate the variability in both distance at first turnaround and pace when escaping. It was not possible to record data blind because our study involved focal animals in the field.

Our measure of fox escape behavior also has similarities with the flight initiation distance from an approaching human, which is commonly recorded to assess boldness or fear towards humans (Cooper and Blumstein 2015; Sih et al. 2023). As the smallest flight initiation distances indicate the boldest reaction and lowest fear level (Blumstein 2003; Sih et al. 2023), so would the smallest distances at first turnaround after release, as foxes stay near humans, which represent a threat, rather than rapidly fleeing away. A fox that stopped and turned around at a small distance from observers, escaping at a slow pace, thus displayed a bold behavior (low fear level), while a fox that turned around at a large distance from observers, escaping at a fast pace, showed a shy behavior (high fear level). The level of fear experienced by individuals should correlate across contexts, such as the exposure to humans, predators, or competitors (Sih et al. 2023). Therefore, we expect that the reaction of individuals towards a human threat should reflect their reaction towards a variety of other threats.

We excluded from analyses all assessments of behavioral reactions from foxes anesthetized during capture (12 observations from 9 foxes, all years combined), as the anesthesia affected their behavior at release. Furthermore, in 2016, when our study was first implemented, we only assessed fox pace and did not measure distance at first turnaround (n = 16). We however found that pace and distance at first turnaround were positively associated in 2017–2019, with individuals using a faster pace being located at a greater distance from the release point at their first turnaround (ANOVA: SS = 2448, $F = 8.55$, $p < 0.001$, $n = 55$; Fig. 1; Tukey HSD post hoc comparisons: fast pace differs from slow and intermediate paces, $p < 0.01$ and $p = 0.02$, respectively, but slow and intermediate paces do not differ statistically, $p = 0.42$). To avoid losing valuable information, we attributed to the 16 observations that lacked the distance at first turnaround the median distance associated to each pace score, calculated from the 55 observations for which both distance and pace had been assessed (i.e., slow = 3 m, intermediate = 6.5 m, fast = 12 m). Distance at first turnaround was the main behavioral trait analyzed statistically since a quantitative variable allows easier interpretation of interaction terms and uses less degrees of freedom. We thus obtained 71 measurements of distance at first turnaround (but see section *Fox reproduction monitoring* for final sample size), from 42 captured foxes observed on average (± SD) 1.7 ± 1.1 times. Twenty-five observations were obtained from 25 individuals observed once, while 46 observations came from 17 individuals with at least two observations (10 individuals observed twice, 3 observed thrice, 3 observed 4 times, and 1 observed 5 times). For the latter, we thus obtained 29 observations considered as replicated measurements, with 8 that were within-year and 21 that were among-year replicates.

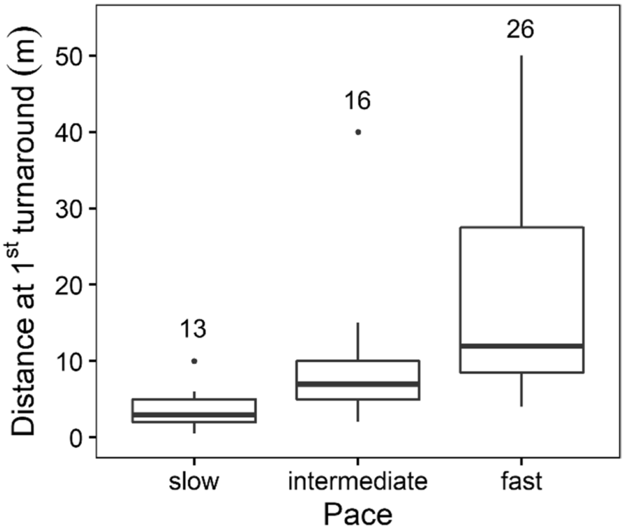

Fig. 1 Fox distance at first turnaround (*m*) as a function of its pace (n = 55) when escaping after handling. Boxplots show first quartile, median, and third quartile. Lower and upper whiskers extend, respectively, to the lowest and highest values within the interquartile range multiplied by 1.5. Points represent values outside this range. Numbers on top of boxes are number of observations for each category

Fox reproduction monitoring

Arctic foxes live as territorial pairs and use dens for reproduction. Arctic fox pups first emerge from their natal den when about 3-week-old (Tannerfeldt and Angerbjörn 1998). The 115 dens located in our study area were visited at least twice in May–August. During the first visit in May, we installed automated cameras (RapidFire Professional PC85 and HyperFire PC800, Reconyx, Holmen, WI, USA) on all dens showing signs of recent activity (digging, hair, tracks, prey remains, presence of adults, or pups). Cameras were retrieved in late July-early August, at the end of the field season. Analysis of pictures from cameras and visual observations at dens allowed us to determine the identity and estimate the litter size of foxes using each den. Following the first observation of pups on the den, we counted the maximum number of pups observed on pictures. Picture analysis showed that the maximum number of pups for a litter is typically recorded 6 days after pup first den emergence (Morin 2015). It is always possible that some pups die before emergence or do not appear on pictures, so the maximum number of observed pups represents the minimum litter size. We used this to quantify reproductive success but note that this may not reflect precisely annual fitness since pups can die later in the breeding season and extra-pair paternity occurs in our study area (Cameron et al. 2011). In addition, we could not separate foxes producing no pup from those producing pups who died before emergence from the den.

Individuals were considered non-breeders (litter size = 0) when they used no den with pups, did not lactate (for females), and when we could ascertain that they did not reproduce outside of the study area. We excluded from analyses one male without known pups and that had a territory outside the study area, for a final sample size of 70 behavioral observations associated with a litter size.

Lemming density and access to the snow goose colony

Lemming density was estimated each year using live-trapping in July and a capture-mark-recapture method (Fauteux et al. 2015; Duchesne et al. 2021). We pooled densities of brown and collared lemmings and used two density categories (low/high) following Duchesne et al. (2021). Densities were low in 2017 and 2018 with < 0.3 lemming/ha, while they were high in 2016 and 2019 with > 1.3 lemming/ha.

For each fox-year, we determined whether the fox territory overlapped the snow goose colony, thus giving access to goose eggs. To do so, the boundaries of the colony were determined annually in late June with a GPS and helicopter (Duchesne et al. 2021). Then, we determined whether the locations of the fox captures, dens, and field observations fell within the colony, adding a 1.75-km buffer outside the colony boundaries to account for short extra-territorial excursions (Chevallier et al. 2020).

Statistical analyses

Determinants of fox boldness

Statistical analyses were performed using R version 3.6.1 (R Development Team 2019). To evaluate causes of variation in Arctic fox boldness, we used a linear mixed model (LMM), using the package glmmTMB (version 1.1.1; Brooks et al. 2017), modeling variation in distance at first turnaround (response variable) according to fixed and random effects. We log-transformed the distance at first turnaround to respect the assumption of normality and homoscedasticity in the model's residuals. We included as fixed effects the individual characteristics sex, age, and mass, the latter indicating body condition despite being confounded by body size. We also controlled for habituation to capture by including the number of times the individual was captured throughout its life at the time of the behavioral assessment, including the captures allowing our tests (hereafter capture number). Fox ID was fitted as a random effect to evaluate individual consistency in boldness. We estimated repeatability of boldness as the proportion of variance in that behavior attributed to differences among individuals (Bell et al. 2009; Nakagawa and Schielzeth 2010), using the R package rptR (version 0.9.22; Stoffel et al. 2017). We estimated both adjusted repeatability using a model including fixed effects, and un-adjusted repeatability using a model only containing the overall intercept and ID as random effect. Confidence intervals (CI) were estimated by parametric bootstrapping. Our repeatability estimates mostly reflect among-year individual consistency in boldness, as behavioral tests were mostly replicated in different years for each individual (21 of 29 replicates are among-year replicates). Note that rptR fits a model using the lme4 package (Bates et al. 2015), rather than glmmTMB. We also included year as a random effect to control for variation among years, but then excluded this variable from analyses as this led to a singular fit (variance estimated at zero, see Bolker et al. 2009).

Litter size as a function of boldness and resource abundance

We modeled litter size (response variable) using a zero-inflated Poisson (ZIP) generalized linear mixed model (GLMM), again using glmmTMB, to solve overdispersion and zero-inflation problems observed in exploratory analyses using regular Poisson or negative binomial GLMMs. Zero-inflated models allow to properly model count data that include more zeros than expected by a Poisson or negative binomial distributions. Specifically, the ZIP GLMM models the response variable as a mixture of two probability distributions: (1) the zero-inflated part which models non-occurrence of the outcome, here fox reproduction (0 = at least 1 pup observed, 1 = no pup observed), with a logit-link binomial distribution, and (2) the count part which models the count data, here litter size, with a Poisson distribution (see Zuur et al. 2009; Blasco-Moreno et al. 2019). Each model part may include different fixed and random effects. We were specifically interested in the count part of the model to better understand how lemming density and boldness interacted to determine litter size.

On the zero-inflated part of the ZIP GLMM, we included as fixed effects lemming density (low/high) and whether the fox had access to the goose colony (yes/no), as both variables affect fox probability to reproduce (Chevallier et al. 2020; Juhasz et al. 2020). We kept the zero-inflated part of the model as simple as possible because preliminary models including more fixed and random effects (see below other effects included on the count part) led to convergence issues and underdispersion.

On the count part of the ZIP GLMM, we included as fixed effects lemming density (low/high), the distance at first turnaround as indicator of fox boldness, and their interaction. We also included confounding variables potentially affecting litter size: whether the fox had access to the goose colony (yes/no), fox age (litter size increases with age in some Arctic fox populations, Di Bernardi et al. 2021), and age^2 representing non-linear age effects related to senescence. We fitted as random effects year and fox ID as some measures were repeated. All continuous variables were centered and standardized (Schielzeth 2010). Overdispersion, zero-inflation and residuals diagnostics were assessed using simulation-based tests in the R package DHARMa (version 0.4.3; Hartig 2021).

Table 1 Results from a linear mixed model with log-distance at the first turnaround as the response variable (*n* = 68 due to missing fixed effect values)

Fixed effect	Estimate [95% CI]	SE	*z*	*p*
(Intercept)	2.05 [1.67, 2.42]	0.19	10.81	<0.001
sex [male]	0.07 [−0.49, 0.64]	0.29	0.25	0.80
mass	−0.18 [−0.46, 0.10]	0.14	−1.25	0.21
age	−0.17 [−0.41, 0.08]	0.12	−1.35	0.18
capture No	0.05 [−0.21, 0.31]	0.13	0.39	0.69

Model reference value is "female" for the variable sex

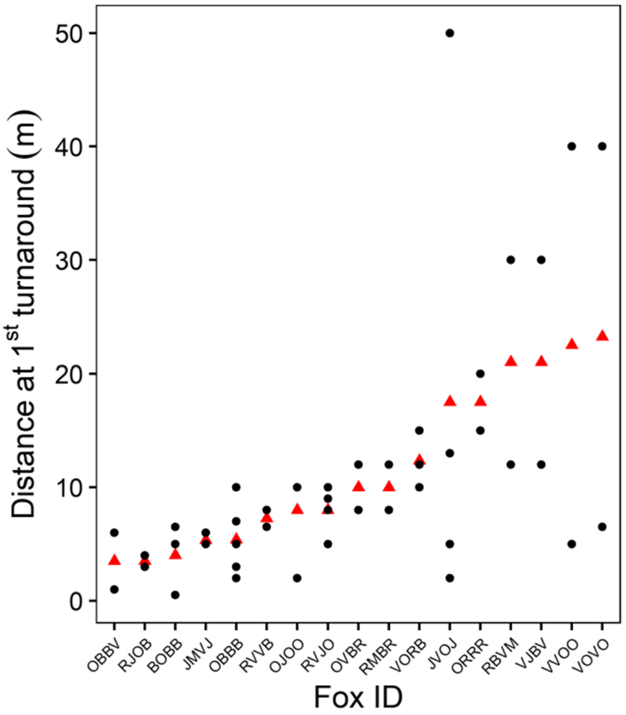

Fig. 2 Distances at first turnaround (black dots) for 17 individuals with more than one behavioral observation (*n* = 46). Red triangles are mean values. Fox IDs reflect the unique combinations of colors of the 4 ear tags (e.g., OBBV = orange-blue-blue-violet)

Results

Determinants of fox boldness

We found no evidence that the fixed effects included in the LMM (sex, mass, age, capture number) had an effect on distance at first turnaround (*n* = 68 due to missing values of fixed effects, Table 1). Adjusted repeatability in fox log-distance at the first turnaround was of 0.19 CI [0, 0.62], whereas un-adjusted repeatability was 0.14 CI [0, 0.47] (*n* = 71). Figure 2 represents individual differences in distance at first turnaround, for the 17 individuals that were observed more than once.

Litter size as a function of boldness and resource abundance

Average (± SD) litter size was 3.8 ± 4.3 pups, with a minimum of 0 (31 out of 70 observations) and a maximum of 14 pups produced. On the zero-inflated part of the ZIP GLMM, we found that lemming density influenced fox probability to reproduce (thus generating the large number of zeros in the dataset). Specifically, in years of low lemming density, few individuals reproduced (Table 2; Fig. 3). However, we found weak evidence of a positive effect of the access to the snow goose colony on the probability to reproduce (Table 2). Then, on the count part of the model, which evaluated determinants of fox litter size, we found a significant effect of lemming density, with high densities leading to larger litter sizes (Table 2). We further found that distance at first turnaround influenced litter size when considered in interaction with lemming density (Table 2). In years of low lemming density, individuals turning at short distances (i.e., individuals exhibiting bold behavior) produced more pups than individuals turning at large distances (i.e., individuals exhibiting shy behavior) (Table 2; Fig. 3). In years of high lemming density, we found no evidence that litter size varied with distance at first turnaround (Table 2; Fig. 3). However, when lemming density was high, most observations yielded lower distances at first turnaround (Fig. 3), which probably reduced our ability to estimate an effect. Regarding the tested confounding effects, as expected, age and age^2 both had significant effects on litter size (Table 2), where litter size increased with age until approximately age 5. We however found no evidence that access to the snow goose colony influenced litter size (Table 2). The dataset contained one apparent outlier, as shown on the right side of the orange area of Fig. 3. Testing the ZIP GLMM without this observation yielded similar results. Excluding observations from year 2016, when we inferred distance at first turnaround from pace, yielded similar results.

Discussion

Boldness in animals is often advantageous on the short term as it increases annual reproductive success (Smith and Blumstein 2008). Temporal variation in environmental conditions may however affect the strength and direction of relationships between behavioral and life-history traits. We indeed found a positive effect of boldness on the litter size of Arctic foxes, but most importantly, this effect depended on the availability of a main prey. When lemmings were scarce, foxes behaving boldly had larger litter sizes

Table 2 Results from a zero-inflated Poisson generalized linear mixed model (ZIP GLMM) with litter size as the response variable ($n = 70$). The zero-inflated part models non-occurrence of reproduction with a logit-link binomial distribution, while the count part models litter size with a Poisson distribution

Model part	Fixed effect	Estimate [95% CI]	SE	*z*	*p*
Zero-inflated	(Intercept)	−2.32 [−3.63, −1.01]	0.67	−3.47	<0.001
Zero-inflated	Lemming density [low]	2.25 [0.87, 3.64]	0.71	3.18	<0.001
Zero-inflated	Colony [no]	1.16 [−0.15, 2.47]	0.67	1.73	0.08
Count	(Intercept)	1.90 [1.67, 2.14]	0.12	15.96	<0.001
Count	Lemming density [low]	−0.86 [−1.34, −0.38]	0.24	−3.53	<0.001
Count	Distance first turnaround	0.07 [−0.11, 0.26]	0.09	0.80	0.43
Count	Lemming density [low]: distance first turnaround	−1.20 [−1.96, −0.44]	0.39	−3.09	0.002
Count	Colony [no]	0.16 [−0.19, 0.50]	0.17	0.89	0.37
Count	Age	0.99 [0.28, 1.69]	0.36	2.74	0.006
Count	Age^2	−1.05 [−1.72, −0.38]	0.34	−3.08	0.002

Fox ID and year were fitted as random effects on the count part of the model. Fixed effects fitted for each part are shown within the table. Model reference values is “high” for the variable lemming density and “yes” for the variable access to goose colony

than foxes behaving less boldly, but this positive effect of boldness disappeared when lemmings were abundant, since foxes then tented to produce larger litters and to exhibit bold behavior. In agreement with Choi et al. (2019), our data pointed to among-individual differences in boldness in Arctic fox, but our small sample size did not allow us to statistically demonstrate that foxes differed consistently in their boldness through time. We also found that individual characteristics, such as sex, age, and mass, did not affect boldness, which stresses the need to identify the sources of variation in the boldness of predators.

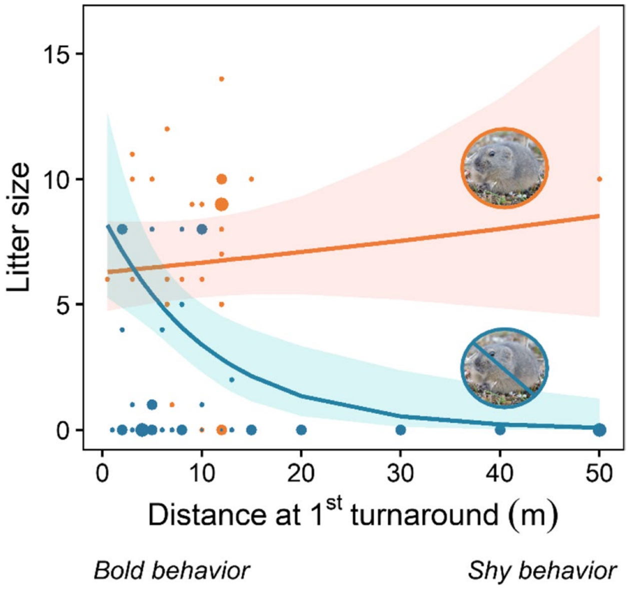

Fig. 3 Arctic fox litter size as a function of distance at first turnaround (*m*) and lemming density (orange = high density, blue = low density), as estimated by the zero-inflated Poisson GLMM ($n = 70$). Levels of boldness (from bold to shy behavior) associated to distances at first turnaround are indicated in italics below the *x* axis. The size of points indicates the number of observations (1, 2, or 3 observations). Shaded areas around slopes are 95% confidence intervals

Weak evidence for consistent among-individual differences in boldness among years

Although males are sometimes bolder than females (Schuett et al. 2010; DeRango et al. 2019), this difference may be more pronounced in sexually dimorphic species compared to monomorphic ones such as the Arctic fox, where sex did not explain variation in boldness after handling. Furthermore, although older individuals are usually bolder than younger ones, which have a higher residual reproduction value (Dammhahn 2012; Bubac et al. 2018), this effect may be more evident when comparing juveniles to adults than when comparing adults of various ages. We also did not observe any effect of body mass on escape behavior after handling, suggesting that body size and condition may not influence boldness in Arctic foxes. However, we could not distinguish the effects of size and condition, and body condition alone could be a better predictor of boldness (Moiron et al. 2019; Moran et al. 2021). Lastly, the number of times individuals were captured did not explain boldness, suggesting that foxes did not habituate to captures and manipulations, which is not surprising given that recaptures were rare and mostly occurred among years.

Choi et al. (2019) observed important within-year among-individual differences in the boldness of Arctic fox, estimating a repeatability of 0.66 CI [0.19, 0.86]. In our study, among-individual variation explained 19% of the variation (adjusted repeatability) in Arctic fox boldness after handling, but the confidence interval was large and included zero. Whether Arctic foxes from our population show consistent among-individual differences in boldness among and within years should therefore be confirmed using larger sample sizes. The first explanation as to why we observed a low repeatability in boldness is that we replicated measures mostly among years (21 of 29 replicates), and personality traits such as boldness are expected to be less repeatable between than within years (Araya-Ajoy et al. 2015). More replicate measures of fox boldness within the same year might yield repeatability estimates equivalent to those found for Arctic foxes by Choi et al. (2019) and also for kit foxes (*Vulpes macrotis mutica*) by Bremner-Harrison et al. (2018). Second, measures obtained upon capture, although useful when studying species hard to observe, may be prone to sampling biases that can reduce the range of possible behaviors and thus among-individual variation and repeatability estimates (Biro and Dingemanse 2009; Biro 2013). For example, the shyest individuals are usually less likely to be trapped than the boldest ones (Réale et al. 2000). In addition, if a boldness-aggressiveness behavioral syndrome was present in the population (Sih et al. 2004), we may have excluded the boldest foxes from the study, as they were possibly the most aggressive and thus the most likely to be anesthetized. Finally, as illustrated in Fig. 2, only some individuals seemed consistent in their distance at first turnaround. Individuals with the shiest reactions overall showed more variation in their escape behavior, suggesting a correlation between behavioral type and level of consistency (shy individuals being more plastic) (Dingemanse et al. 2010). Nevertheless, our results represent an important step forward as very few studies have evaluated the effect of individual characteristics and consistent among-individual differences on the boldness of canid species or other high-trophic level predators, possibly because they are so difficult to observe and capture in large numbers.

Prey availability determines the effect of boldness on reproductive success

Variation in prey abundance strongly influenced the relation between boldness and litter size. When lemming density was low, foxes showing shy reactions produced no pup whereas foxes showing bold reactions had up to 8 pups. Our measure of boldness could relate to risk-taking while foraging (e.g., Dammhahn and Almeling 2012), where boldness may facilitate energy acquisition during reproduction, but this remains to be tested. Acting boldly may allow foxes to acquire lemmings, birds, and eggs at higher rates, for example by hunting lemmings closer to territory edges or by attacking more often adult geese despite their aggressive nest defense (Bêty et al. 2002). Our model predicted a positive effect of the access to the goose colony on the probability to reproduce but the evidence was weak ($p = 0.08$, Table 1), probably because of our low sample size compared to the study of Chevallier et al. (2020). Our results further suggest that access to the goose colony does not affect litter size. However, such an effect on litter size may depend on lemming density, and we did not test the interaction between lemming density and the access to the colony to avoid using more degrees of freedom. Based on our work, further investigations with larger sample sizes will allow the robust test of clear predictions regarding how the access to the goose colony interacts with lemming density and fox boldness to determine fox litter sizes.

Bold foxes may also be the most active and the ones with higher exploratory tendencies (Sih et al. 2004; Mazué et al. 2015). Greater activity and exploration levels may allow foxes to find alternative types of food when lemmings are scarce, thus increasing food intake. Importantly, exploration on the sea ice allows foxes to find alternative prey such as marine mammals (Gagnon and Berteaux 2009; Tarroux et al. 2012; Lai et al. 2015). In contrast, foxes showing a low level of boldness may not be able to access such alternative resources and may thus not be able to reproduce when lemmings are scarce. So far, only a handful of studies have associated predator behavioral types to their foraging performances, using laboratory or mesocosm experiments (e.g., Ioannou et al. 2008; Chang et al. 2017). Furthermore, how hunting abilities explain reproductive success of high-trophic level predators is also largely unknown (but see Jeanniard-du-Dot et al. 2017). For species occupying lower trophic levels, such as insectivorous birds, parental food provisioning mediates the relationship between personality and reproductive success (Mutzel et al. 2013; Thys et al. 2021). A better understanding of how predator behavioral types affect prey capture rates in the wild is required to identify pathways linking behavioral and life-history traits, thus enlightening ecological and evolutionary consequences of variation in the behaviors of predators. This may become possible using sophisticated technologies, such as GPS combined with accelerometers, which might allow detailed assessments of predator behaviors (Hertel et al. 2020; Clermont et al. 2021) and estimation of kill rates (Studd et al. 2021), combined with detailed monitoring of individuals' life-history.

We found no evidence for reproductive benefits of higher boldness level under high food abundance. This underlines the importance of lemmings for the successful reproduction of (all) Arctic foxes. We should however be cautious in interpreting the lack of relation between boldness and litter size during years of high lemming density, as during those years, all observations but one showed bold behavior, thus resulting in a large confidence interval for large distances to first turnaround values (Fig. 3, right part of the orange area). Again, a larger sample size would be necessary to confirm that litter size does not vary with boldness under high prey abundance. The fact that most foxes exhibited bold behavior when resources were abundant is also interesting in itself as it suggests that (1) foxes may have responded to the high lemming abundance by adopting bolder behaviors, or (2) boldness is state-dependent. Future studies should investigate whether predators show plastic responses and adjust their boldness with environmental conditions such as prey availability, or if boldness actually depends on reproductive output (i.e., the state) and not the other way around as we assume in this manuscript.

Overall, our results suggest that temporal environmental variation influences the relationship between a behavioral and a life-history trait in a predator. Assuming Arctic fox level of boldness to be repeatable within years (Choi et al. 2019), boldness brings reproductive advantages to Arctic foxes under low prey availability, potentially because it allows them to acquire more food or alternative resources when their main prey is scarce. Given our results, we could expect positive selection on Arctic fox boldness, with selection strength fluctuating in time. However, bolder Arctic foxes may suffer survival costs, while shyer foxes may save energy by skipping reproduction during years of low food abundance, which could increase their lifespan and lifetime reproductive success. Testing this hypothesis will be challenging as it requires repeated measures of multiple traits for many individuals, ideally over their entire lifespan. However, such a test would greatly increase our understanding of the mechanisms leading to the maintenance of personality differences in animal populations.

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Data availability The dataset is available on Dryad repository at https://doi.org/10.5061/dryad.zcrjdfngj.

Declarations

Ethical approval All applicable national and institutional guidelines for the use of animals were followed. Capture techniques and immobilization procedures were approved by the UQAR Animal Care Committee (CPA-64-16-169), and field research was approved by the Joint Park Management Committee of Sirmilik National Park of Canada (SIR-2018-28021).

Conflict of interest The authors declare no competing interests.

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