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Experience buffers extrinsic mortality in a group-living bird species

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Extrinsic mortality has a strong impact on the evolution of life-histories, prey morphology and behavioural adaptations, but for many animals the causes of mortality are poorly understood. Predation is an important driver of extrinsic mortality and mobile animals form groups in response to increased predation risk. Furthermore, in many species juveniles suffer higher mortality than older individuals, which may reflect a lower phenotypic quality, lower competitiveness, or a lack of antipredator or foraging skills. Here we assessed the causes of mortality for 371 radio tagged Siberian jays. This sedentary bird species lives in family groups that contain a breeding pair as well as related and unrelated non-breeders. Ninety-five percent of death were due to predation (n = 59 out of 62 individuals) and most individuals were killed by *Accipiter* hawks. Multivariate Cox proportional hazards models showed that non-breeders had a lower survival than breeders, but only in territories in managed forest with little visual cover. Examining breeders, only sex influenced survival with males having a lower survival than females. For non-breeders, juveniles had lower survival than older non-breeders, and those on managed territories had lower survival than those on unmanaged territories. Additionally, a low feather quality reduced the survival probability of non-breeders only. Thus, living on managed territories and having a low feature quality affected only non-breeders, particularly juveniles. These findings add to previous research demonstrating that juvenile Siberian jays acquire critical antipredator skills from experienced group members. Thus, experience can buffer extrinsic mortality, highlighting that group living not only provides safety in numbers, but also provide social opportunities to learn critical life-skills.

Extrinsic mortality is an important selective agent influencing the evolution of life-histories, prey morphology and behavioural adaptations (Roff 1992, Newton 1998, Caro 2005). In many species, predation is a major contributor to extrinsic mortality, both directly (Caro 2005, Valcu et al. 2014) and indirectly, through the tradeoff between the time allocated to foraging and the investment in antipredator behaviours (Kaitala et al. 1989, Stankowich and Blumstein 2005). Group-living allows individuals to reduce both the predation risk and the costs of antipredator behaviours through several independent mechanisms (Krause and Ruxton 2002, Caro 2005). It enhances predator detection (Bertram 1978), increases foraging efficiency by reducing individual vigilance (Pulliam 1973), and during a predator attack, provides further benefits through risk dilution (Hamilton 1971) and the confusion effect (Miller 1922).

A large number of field studies have demonstrated that living in groups provides ample antipredator benefits (Caro 2005). Nevertheless, the importance of different causes of mortality remain poorly understood in most animal species, limiting our understanding of the impact of different selective forces on the evolution of group-living (Krause and Ruxton 2002, Caro 2005). Juveniles (i.e. fledged individuals during their first year of life) typically have higher mortality than older individuals (Sullivan 1989, Newton 1998), which is often a consequence of higher predation risk for juveniles (Covas et al. 2004, Gruebler and Naef-Daenzer 2010, Tarwater and Brawn 2010). In animals with slow body growth, such as fish, reptiles and mammals, the high juvenile mortality may be a consequence of an increased predation pressure on smaller individuals (Werner and Hall 1988). In species where individuals rapidly reach adult body size, such as birds, high juvenile mortality may reflect low phenotypic quality, leading to selective disappearance of low quality individuals (Naef-Daenzer et al. 2001), or age-dependent social dominance where adults are dominant over juveniles (Sullivan 1989). Acting in synergy with the former mechanisms, juveniles may lack foraging (Marchetti and Price 1989) or antipredator skills (Griffin 2004, Griesser

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†deceased.

and Suzuki 2016), increasing their mortality. Because group-living constitutes an effective way for the social acquisition of life-skills (van Schaik and Burkart 2011), it may have been promoted by ancestrally high predator-induced mortality, particularly in inexperienced juveniles.

Here we use data from our long-term study on the Siberian jay *Perisoreus infaustus* to investigate the causes of mortality and how social, individual and environmental factors influence mortality. This bird species lives in cohesive groups occupying year-round territories in boreal forests across the Northern Palearctic (Griesser et al. 2006). In addition to the dominant breeding pair, groups can include up to five related and unrelated non-breeders, from up to three different cohorts (mean group size = 3.05, range 1–7) (Ekman and Griesser 2016). About 40% of pairs breed successfully each year (Eggers et al. 2006) and in successful broods, socially dominant offspring expel their subordinate siblings from the parental territory 1–2 months after fledging (Ekman et al. 2002). Subordinate siblings disperse and settle into other groups mostly as non-breeders while dominant juveniles remain on the parental territory up to three years beyond independence (Griesser et al. 2014). Parents provide retained offspring with access to food (Griesser 2003), safe locations during foraging (Nystrand 2006, 2007), and increased antipredator protection during predator encounters (Griesser and Ekman 2004, 2005). This nepotistic antipredator protection has been suggested to reduce the mortality of retained offspring during their first winter (Griesser et al. 2006).

Against this background, we first describe the variation in predator encounter rates in summer (March–August) and winter (September–February, i.e. the two periods of the year when we surveyed the survival of radio-tagged individuals) across our study sites. Secondly, we use Cox proportional hazards models to investigate how social (rank, group size, group composition, kinship), individual (sex, age, individual condition, body size) and environmental factors (habitat structure, predator abundance) influence mortality (see Table 1 for a descriptions of our models and detailed definitions of all parameters). We assessed mortality with the help of radio-tags. This method provides an unbiased assessment of causes of mortality if all deceased individuals are recovered, as was the case in this study.

Based on an earlier study, we hypothesize that non-breeders and individuals living in managed, more open territories experience a higher mortality than breeders and individuals living in unmanaged territories with a high degree of visual cover respectively (Griesser et al. 2006). Since males exhibit more risky behaviours, for example during predator mobbing (Griesser and Ekman 2005), we predict that they experience higher mortality than females (Nystrand et al. 2010). Also, individuals in smaller groups are expected to experience a higher mortality than individuals in larger groups (Roth et al. 2006), and higher predator encounter rate should increase mortality rates. Finally, we investigated the factors that are specifically associated with breeder and non-breeder mortality to also assess the role of group composition and

Table 1. Description of the predictors considered in this study. sqrt: square root transformed factors, ID: individual; obs: number of radio-tagging events; n events = no. of deceased individuals.

Predictors	Description	Predictions
Age	minimum age of focal individual; breeder only and non-breeder only models	juveniles are predicted to have a lower survival than older individuals
Feather quality	the maximum number of faulty growth bars found on a single wing feather	juveniles with a high maximum number of faulty growth bars in wing feathers have a reduced survival (Griesser et al. 2006)
Group composition	breeder only models: groups without non-breeders, groups include only immigrants, groups include at least one retained offspring	breeders in kin groups may have increased survival due to nepotistic antipredator investment
Group size	size of group during the surveyed period; if several birds were radio-tagged simultaneously and one bird died in the first half of the period the other bird was followed, we excluded the deceased bird for the group size count of the second bird	individuals in larger group should experience higher survival due to risk dilution, enhanced vigilance or the confusion effect
Habitat structure	proportion of unmanaged forest on each territory	hawks locate jays more easily in open territories, increasing the predation risk (Griesser and Nystrand 2009)
Kinship	non-breeder only models: retained offspring, immigrant	retained offspring have a higher survival than immigrant non-breeders (Griesser et al. 2006)
Phenotype	breeder only models: retained individuals; immigrants; unknown dispersal timing (see methods)	retained individuals have a higher survival than immigrants (Ekman and Griesser 2016)
Predator encounter rate	average daily encounter rate of predators in the managed and unmanaged part of the study site in summer and winter	a high predator encounter rate is predicted to reduce survival
Rank	breeder; non-breeder	breeders are predicted to have a higher survival than non-breeders
Season	summer (survival followed between March and August), winter (survival followed between September and February	more predators are present at the study site during the summer half of the year, lowering the survival
Sex	female; male	males take more risks than females and thus, are predicted to have a lower survival than females
Tarsus length	tarsus length in mm	larger individuals could have a higher survival

age (breeders only model) respectively kinship and age (non-breeders only model) on mortality.

Material and methods

Data for this study were collected from a long-term study population of Siberian jays near Arvidsjaur (65°40′N, 19°0′E) in northern Sweden (Ekman and Griesser 2016). Here we use data collected from spring 1996 to autumn 2004, and from spring 2011 to autumn 2013, including survival data on 371 individuals from 75 territories. All birds in the study population were individually colour-ringed (Griesser et al. 2012), with the exception of five individuals. Blood (50 µl) was taken from all individuals for molecular sex (Griffiths et al. 1998) and kinship (Griesser et al. 2015) determination. Radio-tagging, blood sampling and handling of birds were performed under the license of the responsible ethics board (Umeå djurförsöksetiska nämd: license number A80-99, A45-04, A50-11).

Assessment of habitat structure

Forests at the study site are typical for the boreal zone of northern Europe and cover a gradient from intensely managed to pristine forests (Griesser and Lagerberg 2012). In managed forests, the entire understory (small spruces, deciduous trees) is removed every 20–40 years to enhance timber production. These forests are therefore more open and provide less visual cover than unmanaged forests, increasing the risk for juveniles of being killed by predators (Griesser et al. 2006). Forests in the northern part of the study site are largely unmanaged (referred to as 'unmanaged part' hereafter), while forests in the southern part of the study site cover a gradient from clear-cuts, plantations, thinned forests to a few unmanaged patches (referred to as 'managed part' hereafter). We used this binary categorization in the analyses concerning the predator encounter rates (see below). In the survival analyses, we included the habitat structure as continuous variable and measured the proportion of unmanaged forest patches that had not been affected by forestry for at least 50 years (Griesser and Nystrand 2009).

Assessment of predator encounter rates

We recorded all predators of Siberian jays that were observed throughout the study period (n = 2300 full days in the field): accipiter hawks (goshawk *Accipiter gentilis*, sparrowhawk *A. nisus)*, owls (hawk owl *Surnia ulula*, boreal owl *Aegolius funereus)*, and pine marten *Martes martes*. Since it was not possible to assess which hawk or owl species had killed a jay, we use predator categories (i.e. hawk, owl, marten) instead of specific predator species. We assessed the daily predator encounter rate in both the managed and unmanaged part of the study site during the two periods of the year when we radio-tagged birds (summer, winter). The predator encounter rates were calculated by dividing the number of encountered predators by the sampling effort in both parts of the study site during a study period (i.e. total number of days spent in each part of the study site, correcting for the number of surveyed territories). Given the large home-range of the main predators and the low predator encounter rates, using number of predators encountered on each territory would not be meaningful.

Mortality assessment and predator identity

We assessed mortality in Siberian jays with the help of radio tags (Holohil BD-2G, Telenax TBX-006, weight 1.8–2.0g, corresponding to 2.0–2.5% of a bird's body mass) glued to the two central tail feathers or mounted with a leg-loop harness (Rappole and Tipton 1991). We mounted tags in March (years 1996–2004, 2011–2013), June–July (years 2000, 2003, 2011, 2013) and in September–October (years 1999, 2001–2004). The tags usually worked for 14–19 weeks, allowing the monitoring of mortality during this period. Tags mounted on the tail dropped off naturally with the next moult, at a maximum of eight months after initial fitting. Birds that had the tag mounted with a leg loop harness were recaptured at the end of the surveying period to remove the radio tag. In total, we attached 586 radio-tags on 371 different individuals. While 238 individuals were tagged once, 75 individuals were tagged twice, 43 individuals three times, 10 individuals four times, one individual five times and four individuals were tagged six times over their lifetime. Individuals tagged in summer were located weekly, while individuals tagged in winter were located at maximum every seven weeks. In winter, remains of deceased individuals were usually buried in snow and therefore remained intact for long periods. Thus, we could identify predator identity and approximate when the individuals were killed (based on how much snow had fallen after the event) even when the remains were located two months after the predation event had occurred. Once the remains of a killed individual were found, predator identity was assessed in the field based on the way the predator handled the prey and the location of the kill (Griesser 2013, Griesser et al. 2006). Hawks pluck their prey on the ground or on an exposed branch (Ferguson-Lees et al. 2001), and faeces, foot or wing prints in the snow help to confirm hawk kills. Owls pluck their prey perched up in dense trees (König et al. 2009) and in most cases we found characteristic pellets (i.e. regurgitated matter consisting of the indigestible remains of the prey) among the remains of the killed bird. Martens leave characteristic bite marks on feathers and colour rings.

Assessment of group size, kinship and age of individuals

Groups were visited repeatedly, both before and after attaching radio-tags, by attracting the birds at established feeding sites, and when monitoring the survival of radio-tagged individuals. During these visits, we recorded the identity of all individuals present. Siberian jay groups are very stable and group members move mostly as a cohesive unit through their territory (Griesser et al. 2006), and readily visit established feeding sites (Ekman and Griesser 2016).

We assessed the kinship of individuals using three methods. In most groups (n = 271 broods) we monitored the reproductive success by following reproduction and banding all nestlings in successful broods (see Eggers et al. 2006 for detailed description of methodology), therefore allowing us to recognize retained offspring. Otherwise, we caught fledglings 1–3 weeks after they had fledged and banded them before dispersal (n = 27 broods). This then meant that all unbanded individuals in these groups had immigrated from elsewhere. Finally, in groups where we did not follow reproduction (n = 130 broods), we assessed relatedness of unbanded group members with molecular methods (details given in Griesser et al. 2015). Most individuals were ringed as nestlings or juveniles, and thus their age was known, while unbanded juveniles can be reliably aged using the shape of the outermost tail feather (Svensson 2006). The exact age of individuals that were banded as adults (n = 98 breeders, n = 2 non-breeders) was unknown, and thus we assigned them an age of two years at the time they settled in the study population.

Assessment of feather fault bars and body size

An earlier study showed that juvenile Siberian jays with a high number of faulty growth bars in their wing feathers had a higher risk of being killed by a predator (Griesser et al. 2006). Faulty growth bars are growth deficiencies (Grubb 2006) that often lead to feather breakage, which in turn impair manoeuvrability and reduce their escape speed during a predator attack (Williams and Swaddle 2003). We counted the number of fault bars on all wing feathers in the field when attaching the radio-tags, and used the tally from the wing feather with the most faulty growth bars in the analyses. We only counted fault bars that covered at least 50% of the feather width. We used the adult tarsus length of all individuals as a proxy for body size (measured with dial callipers to the nearest 0.1 mm).

Statistical analysis

Statistical analyses were carried out in R ver. 3.2.2 (<www.r-project.org>). We assessed the effect of season (summer, winter; categorical variable) and habitat type (managed, unmanaged; categorical variable) and their interaction on the predator encounter rate using a generalized linear mixed model with a Poisson error distribution and the log link function in the stats package (<www.r-project.org>). We included year (categorical variable) as random parameter into this model and used the sampling effort (i.e. number of days and number of surveyed territories per season in each part of the study site) as offset. We evaluated the significance of the random effect year using a likelihood ratio test (LRT) where $-2\times\Delta$ log-likelihood of the model, with and without the random factor year, is tested against a χ^2-distribution with df = 1.

The survival probability of radio-tagged individuals was analysed using Cox proportional hazard models in the package coxme (Therneau 2015) and the package survival (Therneau 2014). These models evaluate the hazard function h(t), which indicates the instantaneous risk of mortality at time t, given survival to time t. They do not assume a normally distributed response variable and can deal with censored data. We investigated the correlates of mortality by running models on all individuals (model 1), breeders only (model 2), and non-breeders only (model 3; see Table 2 for the models and details on the predictors used). Prior to running the models, we checked each response variable for its distribution and applied an appropriate transformation to obtain approximately symmetrical distributions (Table 2). All continuous variables were centred (around the mean) and scaled (by the standard deviation) to facilitate the comparison of effects of explanatory variables (Schielzeth 2010).

We used the number of weeks an individual was followed from radio-tagging to last observation or the time of death in a given radio-tagging period as time to event. For the analyses on all individuals and breeders only we ran mixed effect Cox models, using the function coxme in the package coxme (Therneau 2015), including individual identity as a random factor. We evaluated the significance of the random effect using a LRT. Because only three non-breeders were tagged repeatedly, we chose to only included the first radio-tagging event of these individuals in the analyses on non-breeder mortality. Hence, this allowed us to run a simple (no random effect) Cox model using the function cox.ph in the package survival (Therneau 2014). The regression coefficients obtained for each model represent the log change in the hazard function per unit increase of the predictor variable. A negative coefficient indicates increased survival chances with an increasing value of the predictor variable. Again, we evaluated the significance of the predictors using LRT.

Cox proportional hazards model assume that the hazard ratio is constant over time. This assumption was both tested on models excluding the random factor using the cox.zph function in the package survival (Therneau 2014), and by conducting graphical diagnostics. To check for collinearity, we calculated the variance inflation factor (VIF) (Dormann et al. 2013) from a linear mixed effect model (all individuals, breeder only analyses) or a linear model (non-breeder only analysis) including all the predictors investigated using the *vif.mer* function (<https://github.com/aufrank/R-hacks/blob/master/mer-utils.R>) and the vif function in the package HH (Richard 2016). The mean VIF of all models were less than 2.1, which indicates an acceptable amount of covariance among predictors. It was not possible to include both rank and age into the model 1 including all individuals, given the high covariance between these two predictors.

Table 2. Structure of the three Cox proportional hazard models.

Model 1	(event,time) = sqrt(predator abundance) + sqrt(habitat structure) + group size + rank + season + sex + rank × sqrt(habitat structure); (n = 371 IDs; 586 obs; n = 62 events)
Model 2	(event,time) = log(age) + sqrt(predator abundance) + sqrt(habitat structure) + group size + group composition + phenotype + season + sex; (n = 256 IDs; n = 448 obs; n = 38 events)
Model 3	(event,time) = age + sqrt(predator abundance) + log(habitat structure) + log(group size) + kinship + season + sex; (n = 135 IDs and obs; n = 24 events)

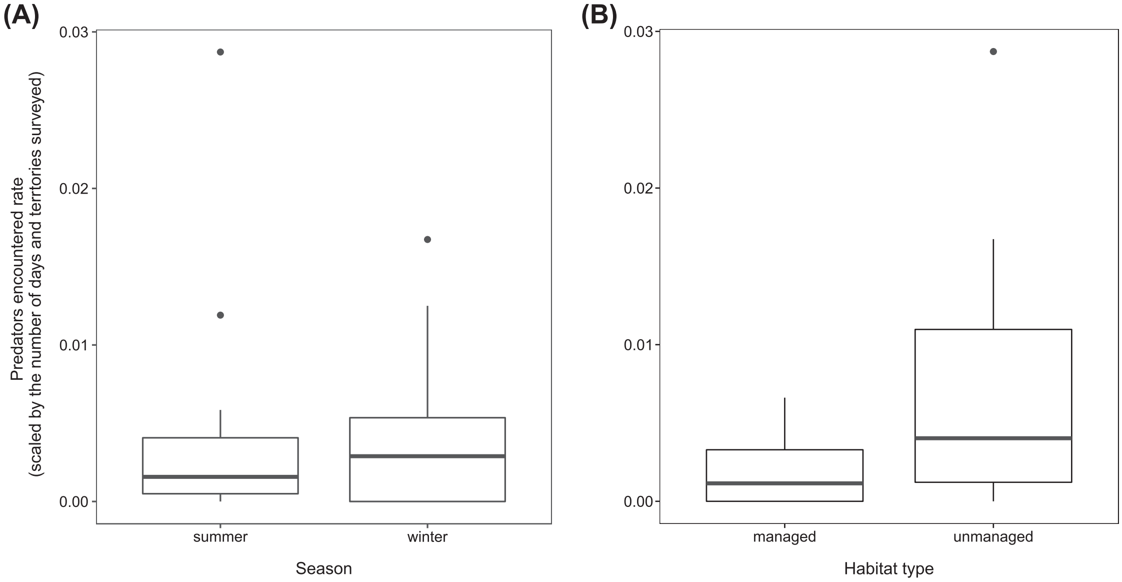

Figure 1. Daily predator encounter rate (scaled by the sampling effort) in (A) summer (March–August) and winter (September–February; i.e. the two periods of the year where we surveyed the survival of radio-tagged individuals), and (B) the managed and unmanaged part of the study site (line in boxes corresponds to median, boxes to 95% third (up) and first (down) quantiles).

We assessed the influence of feather quality and body size on mortality by re-running the three survival models on a subset of individuals for which these data were available. We included the maximum number of faulty growth bars in wing feathers at the time of attaching the radio-tag and the tarsus length of an individual into these models.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.83r81> (Griesser et al. 2017).

Results

Predator encounters

We encountered predators on 128 occasions during the 12 years where we mounted radio-tags (Fig. 1). Goshawks (n = 45) and sparrowhawks (n = 41) were the most frequently observed predators, while owls (n = 20) were less frequently encountered. We observed only one pine marten but recorded two nests that were predated by this species. Another 19 encounters involved hawk-sized birds of prey, but the species could not be identified. Sparrowhawks are migratory at the study site, and thus, they were only observed between late April and early September. The average daily encounter rate varied between 0 and 0.03 predators per day and territory (mean = 0.004; Fig. 1), and more predators were encountered during winter and in the unmanaged part of the study site (Fig. 1i–ii; Table 3) than during summer and the managed part of the study site. Also, the encounter rate varied substantially between years (Table 3).

Causes of mortality

All radio-tagged individuals were recovered and 59 out of 62 individuals were the victim of predation. Only 3 individuals

Table 3. Predator encounter rate analysis. Effect of year, season, habitat type and the interaction between season and habitat type on the predator encountered rate. Estimates and standard errors (SE) are presented. Significant effects are highlighted in bold. The p-value for the effect of year was tested using a likelihood ratio test (LRT) between a model including versus excluding year.

	Effect size levels (categ. variables)	Estimate	SE	z-value	p-value
Intercept		**–6.12**	**0.28**	**–22.10**	**< 0.0001**
Season	**winter**	0	na		
	summer	**–0.62**	**0.23**	**–2.64**	**0.008**
Habitat type	**managed**	0	na		
	unmanaged	**0.84**	**0.30**	**2.81**	**0.005**
Season × Habitat type	winter × managed	0.00	na		
	winter × unmanaged	0.00	na		
	summer × managed	0.00	na		
	summer × unmanaged	0.00	0.38	–0.01	0.99
Random effect	variance	SD	LRT	df	p-value
Year	**0.44**	**0.67**	**33.22**	**1**	**< 0.0001**

na – not applicable; levels of categories with ‘na’ are the reference levels.

Table 4. Causes of mortality of 372 Siberian jays (587 tagging periods). Individuals were followed on average for 13.7 weeks, or until found dead. Three individuals were found dead on the ground between early April and early May without any sign of interactions with predators.

Status	n breeders	N non-breeders
Survived	412	114
Killed by hawks	24	18
Killed by owls	8	4
Killed by hawk or owl	2	0
Killed by pine marten	1	2
Found dead on ground	3	0
Total died	38	24
Proportion died (%)	8.5	17.3
Total n	449	138

(5%) were found dead on the ground without any sign of predation. Predator category could be identified in 57 cases (97%; Table 4): Hawks killed the majority of individuals (n = 42 individuals), owls were responsible for 12 kills, and pine martens killed three individuals. Two individuals were killed by an avian predator, but it was impossible to determine whether they were killed by a hawk or an owl.

Correlates of mortality

A survival model including all individuals showed that non-breeders had a lower survival than breeders (Fig. 2). However this effect depended on the habitat structure, and only non-breeders living in more open territories with a low proportion of unmanaged forest had a lower survival than breeders (Fig. 3). Also, individuals had a comparatively lower survival in winter than in summer (Fig. 3). Separate analyses for breeders and non-breeders, also including age and rank specific social factors, largely confirmed these results. Among breeders, males experienced a lower survival than females, but no other putative factor influenced their survival (i.e. group composition and size, age or habitat quality; Table 5). Among non-breeders, survival was lower on territories with a low proportion of unmanaged forest (Table 5). Moreover, older non-breeders had higher survival than juvenile non-breeders (Table 5, Fig. 4), but neither kinship nor group size affected their mortality (Table 5). Thus, because non-breeders had higher mortality rates than breeders, this implies that juveniles had the highest mortality of all age classes. Models that also included feather quality and body size confirmed these findings, but showed that a high number of growth deficiencies in the wing feathers reduced the survival of non-breeders but not breeders (Table 6).

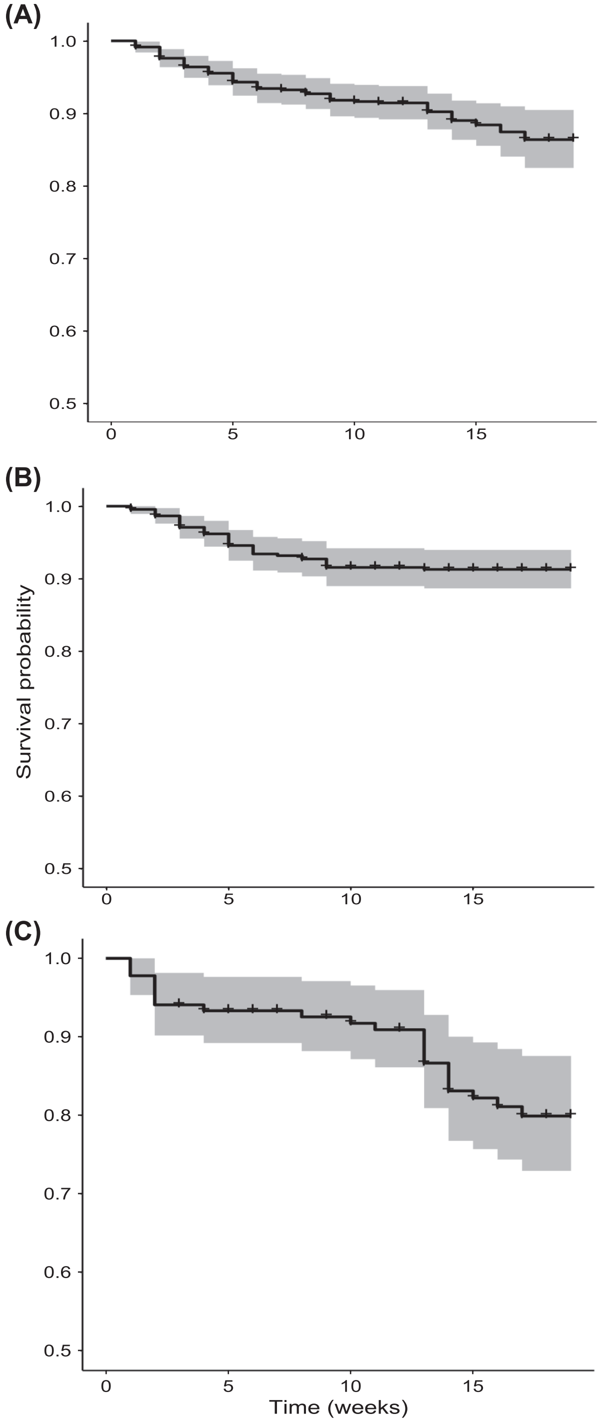

Figure 2. Kaplan–Meier survival curves of Siberian jays: all individuals (A), for breeders only (B), for non-breeders only (C). The grey zones indicate the 95% confidence intervals.

Discussion

Our results show that predation was the primary cause of mortality of 372 radio-tagged Siberian jays, with only 3 out of 61 individuals found dead without signs of predation. These findings confirm the critical role of predation as a source of extrinsic mortality in birds (Newton 1998, Caro 2005, Valcu et al. 2014). Other studies highlighted that disease is an important cause of mortality in many species (Scott 1988), including birds (Newton 1998). However, we only exceptionally observed individuals that appeared to be sick, and in only one case did this lead to that the individual disappeared (MG unpubl.). Notably, juveniles had substantially higher mortality than older non-breeders and breeders, but only in managed territories with little visual cover. Similarly, a low feather quality was associated with a high mortality only in juveniles. These findings suggest that older individuals are able to cope with living in more open

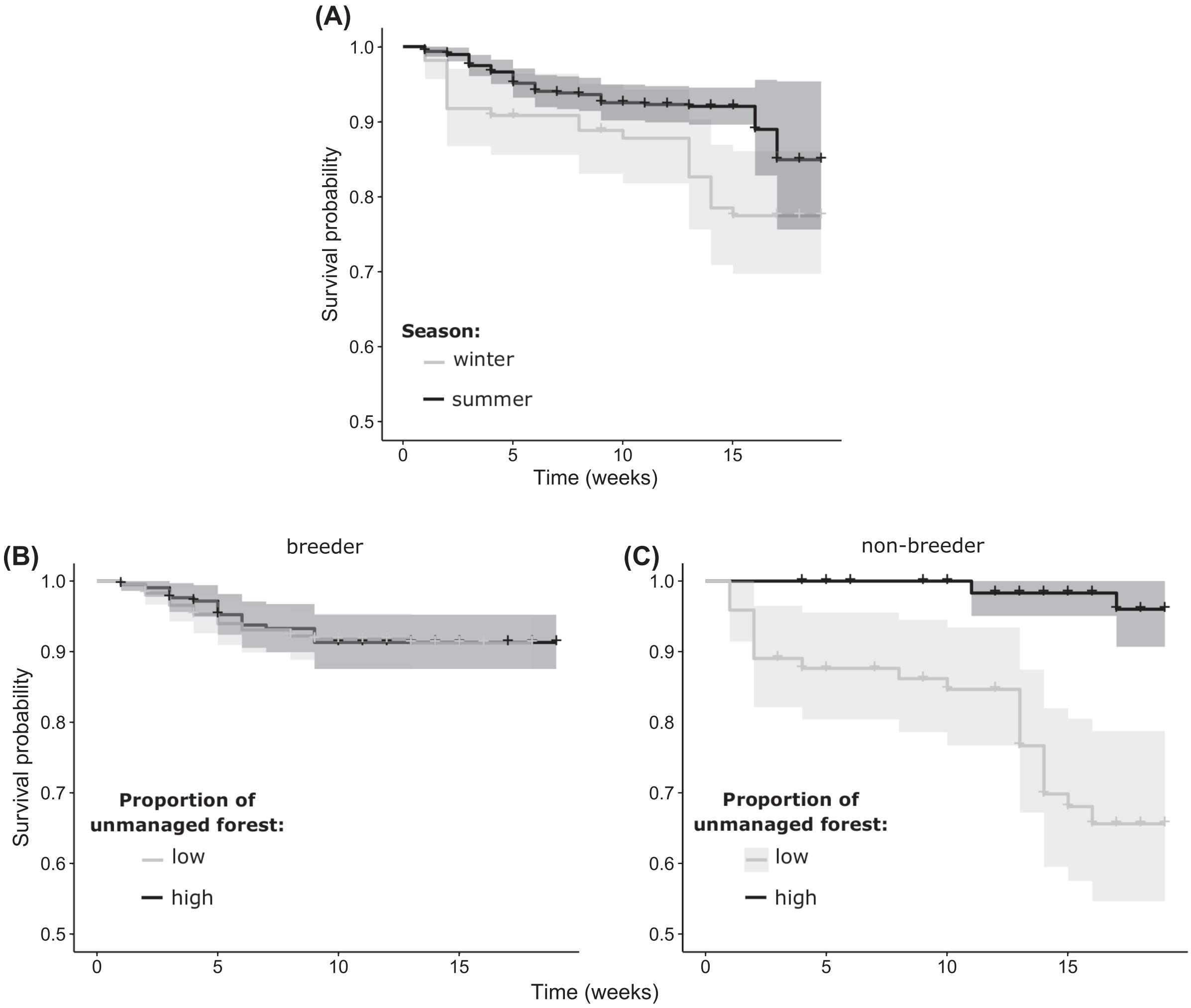

Figure 3. Kaplan–Meier survival curves of all birds depending on (A) the season, and the interaction between rank (breeder (B), non-breeder (C)) and habitat structure (displayed as binary variable based on a median-split method). The grey zones indicate the 95% confidence intervals.

territories and a low feather quality either because of experience or social dominance, or that juveniles that die are of low phenotypic quality, leading to the selective disappearance of low quality individuals.

The main predators of Siberian jays, *Accipiter* hawks, are visual ambush hunters (Kenward 1978) and locate prey more easily in open forests. In our population hawk attacks were only observed in managed territories (Griesser and Nystrand 2009) and during attacks, these forests provide less cover to escape. Nevertheless, living in territories with little cover increased mortality only in juvenile jays. Juveniles do not respond to hawk models when exposed to them in absence of older individuals (Griesser and Suzuki 2016), and during simulated hawk attacks, juveniles have a longer reaction time than breeders (Griesser 2013). However, all juveniles that observe knowledgeable group members mobbing a goshawk model survived their first winter (Griesser and Suzuki 2017). These findings support the notion that the high juvenile mortality reflects a lack of antipredator skills. Thus, observing knowledgeable individuals interacting with predators may be critical for naïve Siberian jays, particularly if predators are rarely encountered, as the case in our study population (Fig. 1).

In addition to lacking predator recognition skills, juveniles may also suffer from a higher mortality due to low social rank or low phenotypic quality. Particularly immigrant juveniles behave in a more risk-prone way than older group members and retained juveniles (Griesser 2003, Nystrand 2006). However, kinship did not influence non-breeder mortality (Table 4), and thus, a low social rank per se does not increase mortality in Siberian jays. In contrast, low feather quality (i.e. a measurement of phenotypic quality) was associated with a higher mortality of non-breeders (Table 5). This difference may be explained by at least two non-exclusive mechanisms. First, a low feather quality increases feather breakage, impairing flight manoeuvrability during predator attacks (Williams and Swaddle 2003). Second, it may reflect a generally low phenotypic quality, whereby low quality individuals might be slower to respond during a predator attack (Cresswell et al. 2003). Unfortunately, it was not possible to assess the state of wing feathers in most killed individuals since we rarely retrieved all wing feathers. We repeatedly captured juveniles that survived their first winter of life with broken feathers,

Table 5. Survival analyses: 1) all individuals, 2) breeders only, and 3) non-breeders only. Significant effects are highlighted in bold. Note that a higher estimate corresponds to a lower survival rate. NB = non-breeders, sqrt = square root transformed factor, log = log transformed factor.

	Effect size levels	Coeff	SE (coeff)	Hazard ratio	χ^2	df	p-value
1) Al individuals							
sqrt (predator encounter rate)		0.01	0.16	1.01	2.10	1	0.15
Group size		0.05	0.15	1.05	0.99	1	0.32
sqrt(habitat structure)		**–0.03**	**0.17**	**0.97**	**5.97**	**1**	**0.01**
Rank	breeder	0	na	0	1.29	1	0.26
	non-breeder	–0.16	0.41	0.85			
Season	**winter**	**0**	**na**	**0**	**4.03**	**1**	**0.04**
	summer	**–0.58**	**0.4**	**0.56**			
Sex	female	0	na	0	1.13	1	0.59
	male	0.36	0.3	1.43			
sqrt(habitat structure) × rank	**breeder**	**0**	**na**	**0**	**6.76**	**1**	**< 0.0001**
	non-breeder	**–0.85**	**0.35**	**0.43**			
2) Breeders only							
log(age)		0.12	0.18	1.13	0.78	1	0.38
sqrt(predator encounter rate)		–0.09	0.19	0.91	0.16	1	0.69
Group size		0.23	0.3	1.26	0.35	1	0.56
sqrt(habitat structure)		0.01	0.18	1.01	0.07	1	0.79
Phenotype	kin	0	na	0	0.50	2	0.78
	non-kin	0.33	0.55	1.39			
	unknown	0.01	0.55	1.01			
Sex	**female**	**0**	**na**	**0**	**4.10**	**1**	**0.04**
	male	**0.77**	**0.4**	**2.17**			
Group composition	no NB	0	na	0	0.34	2	0.84
	kin NB	–0.44	0.75	0.65			
	nk NB	–0.29	0.59	0.75			
Season	winter	0	na	0	0.00	1	0.96
	summer	–0.04	0.75	0.96			
3) Non-breeders only							
Age		**–8.00**	**2202**	**0.00**	**4.15**	**1**	**0.04**
sqrt(predator encounter rate)		0.08	0.32	1.08	0.03	1	0.87
log(group size)		0.16	0.23	1.18	0.15	1	0.70
log(habitat structure)		**–0.68**	**0.21**	**0.51**	**12.95**	**1**	**< 0.001**
Sex	female	0.00	na	0.00	0.08	1	0.78
	male	0.08	0.42	1.09			
Kinship	kin	0.00	na	0.00	1.63	1	0.20
	non-kin	0.46	0.44	1.58			
Season	winter	0.00	na	0.00	1.05	1	0.31
	summer	–0.64	0.65	0.53			

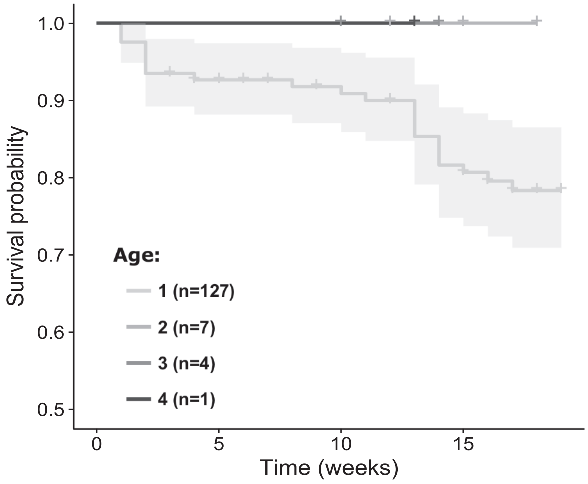

Figure 4. Kaplan–Meier survival curves of non-breeders depending on their age. The grey zones indicate the 95% confidence intervals.

suggesting that feather breakage alone does not account for the recorded increase in mortality. Importantly, a low feather quality did not affect mortality among older individuals, showing that they can cope with this handicap.

In contrast to many other studies (Caro 2005), group size does not influence mortality in Siberian jays. This pattern is remarkable since safety in numbers is particularly efficient in small groups where an additional group member reduces the individual risk substantially more than in larger groups (Roth and Lima 2003, Roth et al. 2006). Given that warning calls during attacks boost non-breeder survival (Griesser 2013), protection by experienced group members may reduce the predation risk of all group members independent of group size. Alternatively, the benefits from safety in numbers may be offset by the costs of living in a larger group, given that predators are more likely to detect a larger group compared to a smaller group (Krause and Godin 1995, Caro 2005). If jays in high-risk, more open habitat were found to live in larger groups, habitat-specific predation rates could be

Table 6. Survival analyses including feather quality and tarsus length: 1) all individuals, 2) breeders only, and 3) non-breeders only. Significant effects are highlighted in bold. Note that a higher estimate corresponds to a lower survival rate. NB = non-breeders, sqrt = square root transformed factor, log = log transformed factor.

	Effect size levels	Coeff	SE (coeff)	Hazard ratio	χ^2	df	p-value
1) All individuals							
sqrt(predator encounter rate)		–0.59	0.30	0.55	1.03	1	0.31
Group size		**–0.49**	**0.20**	**0.61**	**11.44**	**1**	**0.0007**
sqrt(habitat structure)		0.54	0.29	1.71	3.73	1	0.053
Rank	breeder	0.00	na	0.00	3.35	1	0.07
	non-breeder	0.42	0.54	1.52			
Season	**winter**	**0.00**	**na**	**0.00**	**5.69**	**1**	**0.017**
	summer	**–1.11**	**0.59**	**0.33**			
Sex	female				0.40	1	
	male	0.19	0.43	1.21			0.53
Tarsus length		0.00	0.19	1.00	0.00	1	0.99
Feather quality		0.24	0.15	1.27	2.06	1	0.15
sqrt(habitat structure) × rank	breeder	0.00	na	0.00	1.74	1	0.19
	non-breeder	–0.50	0.37	0.61			
2) Breeders only							
log(age)		0.31	0.28	1.37	0.18	1	0.68
sqrt(predator encounter rate)		–0.59	0.32	0.56	1.01	1	0.31
Group size		0.67	0.41	1.95	3.35	1	0.07
sqrt(habitat structure)		–0.15	0.29	0.86	0.22	1	0.64
Phenotype	kin				4.42	2	0.11
	non-kin	2.06	1.21	7.83			
	unknown	0.95	1.19	2.59			
Sex	female	0.00	na	0.00	2.75	1	0.10
	male	1.10	0.89	3.01			
Group composition	no NB	0	na	0.00	4.31	2	0.12
	kin NB	–0.99	1.16	0.37			
	nk NB	0.48	0.87	1.61			
Season	winter						0.86
	summer	–0.22	1.24	0.80	0.03	1	
Tarsus length		0.14	0.32	1.15	1.22	1	0.27
Feather quality		–0.31	0.39	0.73	0.72	1	0.40
3) Non-breeders only							
Age		–3.48	1074.85	0.03	0.97	1	0.33
sqrt(predator encounter rate)		–0.25	0.38	0.78	1.27	1	0.26
log(group size)		0.20	0.23	1.22	0.34	1	0.56
log(habitat structure)		**–1.18**	**0.37**	**0.31**	**17.13**	**1**	**0.00003**
Sex	female	0	na	0	0.00	1	0.98
	male	0.02	0.50	1.02			
Kinship	kin	0.00	na	0.00	2.46	1	0.12
	non-kin	0.66	0.45	1.93			
Season	winter	0	na	0	0.29	1	0.59
	summer	–0.41	0.78	0.67			
Tarsus length		0.08	0.26	1.08	0.10	1	0.75
Feather quality		**0.68**	**0.23**	**1.97**	**8.21**	**1**	**0.004**

obscuring the link between group size and mortality rates. Yet, our analyses show that group size and habitat structure were independent of each other (VIF for both factors smaller than 1.8).

Conclusions

Insights into the causes of mortality are important in understanding demography and the evolution of life-history traits (Stearns 1992). Our results support the notion that mortality in birds is largely driven by predation (Newton 1998, Valcu et al. 2014), and highlight that experience has a large impact on mortality (Marchetti and Price 1989, Mumme et al. 2000, Schuppli et al. 2012). Species that live in predator free environments, such as seabirds, experience low extrinsic mortality (Valcu et al. 2014), contributing to their extraordinary long lifespans and associated slow life-history pace (Mourocq et al. 2016). Yet, individuals in species that regularly encounter predators on their own have a high risk of being killed, making individual learning difficult (van Schaik 2010). Group living can directly provide safety in numbers (Caro 2005) but may also provide inexperienced individuals with a safe haven to acquire critical life-skills (van Schaik and Burkart 2011, Loukola et al. 2013, Griesser and Suzuki 2017). Finally, living in habitats that provide protection from predators can buffer the predation risk of inexperienced individuals, which may explain the accelerated population declines of many species living in managed habitats, not only in the tropics but also in boreal forests (Monkkonen 1999, Eggers and Low 2014, Virkkala 2016).

In a number of bird species, juveniles have a high mortality in more open habitats (Cox et al. 2014), leading to population declines in these habitats (Sisk et al. 1994, Davies et al. 2000). Thus, changing forestry management strategies away from clear-cutting and thinning regimes, towards more green continuous forestry practises (Gustafsson et al. 2010) is likely to improve juvenile survival in forest dwelling species, and hence, have potentially large positive effects on their population dynamics.

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