RESEARCH ARTICLE

Early-life diet specificity is associated with long-lasting differences in apparent survival in a generalist predator

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Abstract

1. Early-life conditions can have long-term fitness consequences. However, it is still unclear what optimal rearing conditions are, especially for long-lived carnivores. A more diverse diet ('balanced diet') might optimize nutrient availability and allow young to make experiences with a larger diversity of prey, whereas a narrow diet breadth ('specialized diet') might result in overall higher energy net gain. A diet that is dominated by a specific prey type (i.e. fish, 'prey type hypothesis') might be beneficial or detrimental, depending for example, on its toxicity or contaminant load.

2. Generalist predators such as the white-tailed eagle *Haliaeetus albicilla* provide an interesting possibility to examine the relationship between early life diet and long-term offspring survival. In the Åland Islands, an archipelago in the Baltic Sea, white-tailed eagles live in various coastal habitats and feed on highly variable proportions of birds and fish.

3. We use data from 21,116 prey individuals that were collected from 120 territories during the annual surveys, to examine how early-life diet is associated with apparent annual survival of 574 ringed and molecular-sexed eaglets. We supplement this analysis by assessing the relationships between diet, reproductive performance and nestling physical condition, to consider whether they are confounding with possible long-term associations.

4. We find that early-life diet is associated with long-term fitness: Nestlings that are fed a diverse diet are in lower physical condition but have higher survival rates. Eagles that are fed more fish as nestlings have lower survival as breeding-age adults, but territories associated with fish-rich diets have higher breeding success.

5. Our results show that young carnivores benefit from a high diversity of prey in their natal territory, either through a nutritional or learning benefit, explaining the higher survival rates. The strong relationship between early-life diet and adult survival suggests that early life shapes adult foraging decisions and that eating fish is associated with high costs. This could be due to high levels of contaminants or high competition for fish-rich territories. Long-lasting consequences of early-life diet are likely not only limited to individual-level consequences but have the potential to drive eco-evolutionary dynamics in this population.

[Correction added on 20 May 2023, after first online publication: The copyright line was changed.]

1 | INTRODUCTION

Early-life conditions can have profound impacts on individual fitness for animals (Cam & Aubry, 2011) and they can affect a wide range of behavioural and demographic parameters even in adult life (e.g. Cam & Aubry, 2011; Cardona et al., 2017; Descamps et al., 2008; Xu et al., 2018). Early-life diet is an essential part of these conditions as post-natal development has high nutritional and caloric demand (Madsen & Shine, 2000). Nutritional restrictions will disrupt somatic development, which can carry over into negative long-term fitness consequences like reduced longevity (English & Uller, 2016; Salmón et al., 2021), faster senescence (Cooper & Kruuk, 2018) or lower reproductive performance (Blount et al., 2006; Descamps et al., 2008; Nowicki et al., 1998).

Following optimal foraging theory, an optimal diet is characterized by maximizing the quantity and quality of food but minimizing the energetic requirements to obtain it (Krebs, 1978; Pulliam, 1974). When evaluating a good diet, emphasis has often been put on calorie or energy net gain (Krebs, 1978; Machovsky-Capuska et al., 2016; Pulliam, 1975; Pyke, 1984). However, foods differ in their nutritional quality in terms of their composition and there are advantages in fulfilling caloric needs from a wider range of foods (Simpson & Raubenheimer, 2012). A diverse early-life diet has been shown to be advantageous in terms of survival in several herbivores and omnivores (i.e. Lee et al., 2012; Lefcheck et al., 2013; Whiteside et al., 2015), and a balanced diet is also a common recommendation for a healthy human diet (nhs.uk, who.int; accessed 2.11.2022). The enhanced nutritional composition obtained through an increased diet diversity appears to be an important contributor to an ideal early-life diet for many animals, as it allows developing young to receive all necessary nutrients for physical and physiological development (Kohl et al., 2015; Simpson & Raubenheimer, 2012).

For a long time, this understanding did not apply to carnivorous species. For them, the prevailing idea has been that they can gain all the necessary nutrients in the right proportion from their main prey (Kohl et al., 2015; Senior et al., 2015). Thus, a predator's only concern has been thought to be successful foraging, not *what* they forage for (Kohl et al., 2015; Machovsky-Capuska et al., 2016). To some extent, this is supported by species that are considered generalists but commonly consist of generalist and specialist individuals (Terraube et al., 2014). In these species, diet specialization is often related to higher reproductive performance (Katzner et al., 2005; Llorente-Llurba, 2019; Otterbeck et al., 2015; Pagani-Núñez et al., 2015), which is explained by specialized individuals being better foragers and catching more food (Terraube et al., 2014). However, the advantage of specialized foraging does not seem to be the general rule (see i.e. Margalida et al., 2009; Navarro-López et al., 2014; Whitfield et al., 2009) and a diverse diet might be associated with benefits for

young as well. Such benefits could be related to physiology, such as better brain development in young (Kitaysky et al., 2006), a more diverse microbiome (Kohl, 2012; Oliveira et al., 2020) or a better immune system (Navarro-López et al., 2014), which can also be good predictors of survival (Bowers et al., 2014; Hegemann et al., 2013, 2015; Kitaysky et al., 2006; Wilcoxen et al., 2010; Worsley et al., 2021).

A higher diversity of different foods in the natal environment can affect young also via different pathways than nutrition (Kohl et al., 2015; Machovsky-Capuska et al., 2016). Benefits could be associated with learning experiences: many species experience sensitive learning windows at a young age (Dufty Jr et al., 2002; English et al., 2016). Encountering a high diversity of suitable prey in the natal area might give young crucial experiences with their prey or promote the development of greater behavioural plasticity (Cardona et al., 2017; English et al., 2016; Solaro & Sarasola, 2019). Such lateral transmission of information from the parent to the offspring can shape an individual's lifelong foraging niche preference and thus have the capacity to determine an individual's adult fitness (Aplin, 2019; Slagsvold & Wiebe, 2011).

Due to difficulties of working with elusive and long-lived carnivores, it remains largely unclear whether early-life diet can have long-lasting consequences and translate into long-term fitness conditions. The white-tailed eagle *Haliaeetus albicilla* is an obligate carnivore of coastal ecosystems and its population of the Åland Islands (Baltic Sea) is highly suitable for such a study because unique data are available from their nestling-time diet and survival. We have previously shown that there is a large variation in the diet of white-tailed eagle nesting in this area, with as many as 99 different prey species identified (Ekblad et al., 2016). Variation in diet is partly related to the spatial position of the nesting territory in the Åland Islands archipelago: In the outer archipelago with much open sea and small islands, the eagle eats almost exclusively avian prey. In the middle and inner archipelago, half or more of the prey can be fish (Ekblad et al., 2016). Different types of prey probably differ in value and cost for white-tailed eagles. From an energetic perspective, preying on fish likely suits the eagle's preferred sit-and-wait foraging mode (Nadjafzadeh et al., 2016; Simpson & Raubenheimer, 2012), but due to the high fat content of waterfowl, waterfowl may provide overall more calories per catch. In addition to the energetic perspective, prey are the primary source of environmental pollutants for white-tailed eagles in the Baltic Sea (HELCOM, 2018). Contaminant composition can vary temporally and spatially but also between species (Airaksinen et al., 2015; Fenstad et al., 2016, 2017; Hallikainen et al., 2004, 2011; HELCOM, 2010). The great variation between pairs in both diet breadth and in what type of prey the diet contains enables us to ask questions both about the importance of variation *per se* and of specific prey species or groups, and their associated environmental conditions.

We examined how different early-life diets might be associated with differences in long-term quality of offspring in terms of their annual apparent survival rates (apparent survival means that survival estimates are accounting for detectability but not permanent emigration from the covered area, Newton et al., 2016). We supplement this analysis by assessing the relationships between diet and reproductive performance, and diet and nestling physical condition ('short-term fitness'), to consider whether they are confounding with possible long-term associations. Specifically, (1) we test how early-life diet diversity might affect offspring annual apparent survival rates (large diet breadth simultaneously reflecting higher prey diversity; narrow diet breadth being associated with lower prey diversity or parental specialization). If a diet breadth is associated with offspring quality, we predict either a positive (benefit by large diet breadth, 'balanced diet hypothesis') or negative (benefit by small diet breadth, 'specialized diet hypothesis') relationship between survival and the diet diversity index. (2) We tested whether annual survival might be related to the proportion of a specific type of prey ('prey type', fish or birds). Under this 'prey type hypothesis', we predict a positive relationship of increasing proportion of one prey type in the diet. In addition to the assessment of early-life diet on long-term consequences, (3) we also tested the aforementioned hypotheses on reproductive performance and nestling physical condition, to evaluate whether the pattern is consistent across various reproductive stages. Due to the strong correlation of diet and other variables such as habitat and prey availability, we discuss results within this larger, more complex framework.

2 | MATERIALS AND METHODS

2.1 | Study area and field procedures

The Åland Islands form a large archipelago in the Baltic Sea between Finland and Sweden (60.179°N, 19.916°E) and are home to about 20% of the total population of white-tailed eagles in Finland (117 territories in 2020, Högmander et al., 2020; Osprey-foundation, unpublished data). Monitoring of white-tailed eagle breeding success and productivity has been conducted since 1976, and the ringing of nestlings on the Åland Islands has been conducted by the White-tailed Eagle working group under WWF Finland in 1981–2019, under the Osprey-foundation from 2020 onwards and on the Åland Islands under the Nåtö biological station from 2019 onward. Here, we use multiple subsets of the total data (breeding success: 1976–2020; timing of breeding, productivity, and nestling data: 2003–2014) for which sufficient prey remain and nestling information is available (see below). We only considered occupied nests and territories in our analysis and a pair was considered to attempt breeding when at least one nest in their territory was decorated (defined as fresh material being brought to the nest). Breeding attempts that resulted in a known fledgling or a live nestling at ringing age (mean = 5 weeks; range = 3–10 weeks; fledging occurs at 11 weeks) were considered successful, since the nests are typically not disturbed after the

ringing event. Brood size was determined based on number of nestlings during ringing, which was conducted by licensed volunteers. The ringing scheme has included one basic metal ring with a unique code on the right leg and a colour ring with an alphanumeric unique colour-engraving combination on the left leg. During ringing, a part of the nestlings were weighted to estimate physical condition, whereas wing length was measured to estimate age (Helander, 1981). The estimated age at ringing was used to calculate the initiation of egg-laying (hereafter 'laying date'; egg-laying happened 38 days before hatching, Fischer, 1982). From 2003 to 2014, a feather for DNA extraction was plucked of each nestling and used to molecular sex and to obtain a microsatellite genotype profile of the nestlings (Dawson et al., 2015; Ponnikas et al., 2013). Post-fledging records were collected by reading the coded rings at winter feeding stations, at nest sites during nest monitoring (from photographs), or opportunistically by the public. Furthermore, the moulted feathers of the adults were collected beneath nesting trees at nest monitoring visits, to allow genetic identification. For genotyping, primers for microsatellite loci used by Ponnikas et al. (2013) and Hailer et al. (2006) were used, and protocols are described in the supplementary material. White-tailed eagles that were ringed as nestlings on the Åland Islands have been resighted after dispersal from their natal territory on the Åland Islands, elsewhere in Finland, Sweden, Germany, Poland, Latvia, and Estonia (Figure S1, Saurola et al., 2003). In total there were 717 visual resightings (Figure S1) and 121 indirect resightings based on genotype that were concentrated on collections from nest sites in Southwest Finland and the Åland Islands.

2.2 | Collection and collation of prey remains and territory characteristics

The prey data, which is composed of 21,116 prey individuals, was collected by T. Stjernberg and other members of the White-tailed Eagle working group in connection with nest monitoring and ringing of nestlings of white-tailed eagles yearly from May to June. Prey remains (bones, pellets, scales, feathers, and hairs) were mainly collected from under the nests but also to a small extent from the nests and under nearby perches between 1978 and 2018. Remains were collected both from nests with successful and unsuccessful breeding attempts. Previous studies have shown that common eider *Somateria mollissima* (21% of all, 77% of all bird prey items, hereafter 'eider') and northern pike *Esox lucius* (12% of all, 47% of all fish prey items, hereafter 'pike') are the most important prey species on the Åland Islands (Ekblad et al., 2016; Sulkava et al., 1997). For the present analysis, the remains have been identified to genus level. This leads to some loss of information in species-rich genera (i.e. *Anas* ducks) but also allowed us to include prey for which species-level identification was not possible. Prey remains that could not be identified to genus-level were included in the analysis as 'unidentified' (about 2.5% of all prey remains). The 'minimum method' (Oehme, 1975) was used to estimate the number of prey items of each species and further

details on prey remain collection and identification can be found in Ekblad et al. (2016). It must be kept in mind that assessing diet based on prey remain collections can be biased in its representation, with smaller prey and fish (with the exception of pike) being underrepresented (Mersmann et al., 1992; Tornberg & Reif, 2007).

We collate prey remains collected in one territory into sums of 5 years, which means that for every breeding attempt, prey remains collected up to 2 years before and 2 years after were considered. Five years adequately reflect the average minimum length of breeding career in this population (mean = 4.1 years, range = 2–11 years; note that this average is based on a 15-year observation period and likely underestimates the actual average length of breeding career in this population because current data only partially cover the life spans of the individuals). Collating prey remains into summaries also comes with advantages: It allows us to increase the sample size and reduce overall error of single-year observations. Some avian prey species, most notably the eider duck, saw an increase in the late 20th century, but it has thereafter been decreasing in the area (Ekblad et al., 2016; HELCOM, 2013b; Kilpi et al., 2015). For the main prey fish species, quantitative data is unavailable, but the stocks seem to have remained overall stable in the area (HELCOM, 2007, 2013a). Collating prey remains is associated with loss of interannual variation (i.e. caused by weather, prey availability, and their interaction) but can still reflect overall trends in prey species abundance and presence. Collations of less than 10 prey remains during this 5-year period were not included in the analyses.

To take into account that different habitats offer different types of prey, we quantified the amount of land around each nest site. We used the proportion of land cover in the vicinity of white-tailed eagle nests, which describes the position of the nest from inner (more land) to outer (less land, more water) archipelago, as described in Ekblad et al. (2016).

2.3 | Diet variables

To explore the 'balanced vs specialized diet hypotheses', we quantify diet breadth by using the Levins' index (Levins, 1968) as the key explanatory variable. Levins' index, or reciprocal Simpson's index, was calculated by the following formula:

$$\text{Levins}' = \frac{1}{\sum_{i=1}^{n} p_i^2},$$

where p_i represents the proportion of the diet represented by each prey genus. The smaller the Levins' value, the more specialized the diet is (Levins' index, numeric, 2.10–15.29, mean = 7.23). On average, white-tailed eagles in these data had 13.6 different genus in their diet over a 5-year period, but this ranged from 4 to 27. To explore the 'prey type hypothesis', we use the proportion of fish (numeric, 0.00–0.88, mean = 0.25) as the key explanatory variable. The proportion of fish is negatively correlated with the proportion of bird species ($r = -0.98$, calculated over a 5-year period, Figure S2), thus proportion of birds represents the inverse relationship. Note that the inverse is not precisely

$r = 1$ due to the low number of mammalian, reptilian and amphibian prey (Ekblad et al., 2016). Number of prey items ranged from 10 to 197 (mean = 47.67) in a 5-year period. Repeatability (R_m) between single year observations was calculated using the 'RPTR' package (Stoffel et al., 2017) and is $R_m = 0.717$, $SE = 0.051$ and $R_m = 0.322$, SE = 0.072 for the proportion of fish and Levins' index, respectively. To assess the influence of habitat, we used the proportion of land cover as the key explanatory variable. As the land cover variable and proportion of fish are also strongly correlated (Ekblad et al., 2016, Figure S2), we fitted the diet explanatory variables proportion of fish and Levins' index together and land cover as a single key explanatory variable separately into the models described below. We assessed their respective influence on reproductive parameters and offspring quality by assessing estimates, standard error, χ^2 values and p-value. A variable was considered to have statistically significant influence if $p < 0.05$.

2.4 | Analyses of breeding performance

A pair's breeding performance was evaluated in three models: the relationship between diet and initiation of egg-laying ('timing of breeding'), whether the breeding attempt was successful or not ('breeding success') and brood size ('productivity'). In the 'timing of breeding model', we used the earliest estimated laying within one brood (Julian day, numeric) as the response variable in a linear mixed model (LMM). In addition to the key explanatory variables, year and territory ID were added as crossed random effects. In the 'breeding success model', the binary value of success (1) or an unsuccessful breeding attempt (0) was the response variable in a binomial generalized linear mixed model (GLMM). In the 'productivity model', we assessed brood size (1–3 nestlings) in a model with binomial distribution. Due to small sample size of broods with three nestlings (14 nests in our dataset, 3%), we pooled broods with 2 and 3 nestlings, thus coded brood size 1 as '0' and brood size larger than 1 as '1'. As covariates, we added the earliest laying date within one brood, which controls for influences of seasonality. In both the 'breeding success model' and the 'productivity model', year and territory ID were added as crossed random effects. Model fit (dispersion and zero-inflation) of models with binomial distribution were checked with the 'DHARMA' package (Hartig, 2022).

2.5 | Offspring quality

The influence of early-life diet on nestling quality was measured in both short-term and long-term fitness traits. Short-term quality was assessed as a nestlings' physical condition ('physical condition model'), which commonly reflects future fledging success and survival in birds (e.g. Morosinotto et al., 2020; Nebel et al., 2021; Ringsby et al., 1998), whereas long-term quality was assessed as annual survival probability. We note here that physical condition is also a way to examine the amount of food (or calories) provided by the parents, as our diet data does not allow us to do this. In the 'physical condition model', nestling body mass was used as the response variable in a LMM. Wing

length was added as a linear and quadratic term to control for age (Helander, 1981). Furthermore, we controlled for sex (factor, male or female), brood size (factor, 1–3) and Julian day of egg-laying (numeric, 46.58–112.16, mean = 77.92, which equates to 19th March). Year and territory ID were added as nested terms to control for siblings from the same nest not being independent observations. Model residuals were visually inspected to assess model fit.

2.6 | Survival analyses

To evaluate how diet affected annual survival rates, we performed a Cormack-Jolly-Seber (CJS) trap-dependent survival analysis by using the 'MARKED' package (Laake et al., 2013). We used a dataset of 574 nestlings that were ringed on the Åland Islands between 2003 and 2014, of which 296 were subsequently resighted again until 2021. Resighting consisted of two types of data: visual detection from ring resightings at any age and genotypic detection from combining DNA collected from the chicks to DNA from feathers shed by parents at the nest site (for protocols see supplementary material). Using this dataset, we ran a set of multiple candidate models, in which annual apparent survival (Φ) contained the key explanatory variables (Levins' index, proportion of fish, in the same and in contrasting models, land cover, and laying date) as additive terms and in an interaction with age, to explore their relationships at different age classes (immature and adult). In addition, we fit the covariates brood size (factor, 1–3), sex (factor, male and female) and age (factor, 0–4 years old = immature, 5 years and older = adult) as a time-varying covariate in all possible combinations. Resighting probability was set as being influenced by an individual's sex, time (factor) and age. As goodness-of-fit testing indicated unequal resighting probability (significant test2.ct, $p < 0.001$; Gimenez et al., 2017; Pradel et al., 2005), we also fit trap dependency as an individual time-varying covariate (Gimenez et al., 2017), and indicated whether an individual was seen in the previous year (excluding the year of ringing). In the white-tailed eagle, this trap dependency likely arises through an individual's experience and behaviour, but also observational bias. Immature eagles might become aware of winter-feeding sites, at which they are then more likely to be resighted (Saurola et al., 2003), whereas adult birds with known nesting locations are more likely to be seen in subsequent years due to their site fidelity. To check for dispersion issues, we exported the data to MARK to calculate median ĉ (Coquet et al., 2009; White & Burnham, 1999). We determined the model with the best fit by AICc comparison.

In a post-hoc analysis, we added another CJS analysis, but used a subset of 162 nestlings, for which we had physical condition measurements. To obtain a physical condition estimation, we used the residuals from a linear model with body mass as the response (continuous) and sex (factor, male or female) and wing length as a linear and quadratic control for size and age. This allowed us to assess the influence of both physical condition (reflecting also the amount of food) and diet parameters on long-term survival.

For all statistical analyses, we used R (v. 4.1.2, R Core Team, 2019). We used the 'GGPLOT2' package for data visualization

(Wickham, 2016) and the 'TIDYVERSE' package for tidying and formatting the data (Wickham et al., 2019). We used the 'LME4' (Bates et al., 2015) and 'MARKED' (Laake et al., 2013) packages for data analysis with support of the 'VEGAN' package to calculate the Levins' index, the 'PERFORMANCEANALYTICS' package (Peterson & Carl, 2020) to assess correlations, the 'DHARMA' package to assess model fit of models with binomial distribution (Hartig, 2022), the 'GGEFFECTS' package to obtain marginal effects (Lüdecke, 2018), and the 'R2UCARE' for goodness-of-fit analysis for the CJS model analysis (Gimenez et al., 2017). All continuous variables were centred around the mean.

2.7 | Ethical statement

All field work procedures like monitoring of white-tailed eagle nests or ringing of nestlings were conducted following the ethical guidelines of the Ringing Centre of the Finnish Museum of Natural History that issues licenses from the Centre of Economic Development, Transport and the Environment. The nestlings in this study were ringed under licenses 246 and 632. Feathers for DNA extractions were collected under licenses from the Finnish Animal Experiment Board (ESAVI-201-05480/Ym 23, ESAVI/3221/04.10.07/2013, ESAI/3021/04.10.07/2017)

3 | RESULTS

3.1 | Probability of survival in relation to early-life diet

The CJS analysis of this dataset revealed potential long-term associations between apparent survival and early-life diet: models including diet breadth and proportion of fish in an interaction with age term had the best fit (see top 5 models, Table 1). Increasing diet breadth was positively associated with apparent annual survival probability, with the beneficial effect being small (estimate = 0.095, SE = 0.035, Figure 1a, Table S1). Visual examination of the interaction between age and proportion of fish revealed that while immature white-tailed eagles did not differ in their survival, the association was stronger in adult white-tailed eagles. In adults, individuals that had been fed on an early-life diet rich in fish showed lower survival (or higher emigration) rates than their conspecifics that had been fed on an early-life diet that contained a low proportion of fish (Figure 1b). Furthermore, nestlings in larger broods had reduced survival rates (mean Φ brood size 1 = 0.84, SE = 0.02; mean Φ brood size 2 = 0.82, SE = 0.02; mean Φ brood size 3 = 0.70, SE = 0.06). Apparent survival was lower in adults (mean Φ = 0.76, SE = 0.03) than immature eagles (mean Φ = 0.84, SE = 0.02). Resighting probability was higher for females and trap aware individuals than males and trap unaware individuals, respectively. The two age classes had similar resighting rates and resighting likelihood decreased with time (for estimates and error, see Table S1). The global CJS model had good model fit and trap-dependent model assumptions were met (test2.cl: $p = 0.827$; test3.

sm: $p = 0.069$, test3.sr: $p = 0.130$, median $\hat{c} = 1.19$). In the post-hoc analysis, nestling physical condition did not explain apparent survival better than the diet variables (Table S2). The top model included proportion of fish in an interaction with age, brood size and sex, the second model also included diet breadth (ΔAICc = 0.90), thus was very similar as with the larger dataset.

3.2 | Associations between diet and reproductive performance

Breeding success was higher in nests where the eagles fed their nestlings a high proportion of fish or occupied territories with more land cover (Table 2, Figure 2, Table S3), whereas diet breadth was not associated with breeding success (Table 2, Table S3). There was strong evidence that egg-laying was initiated earlier in territories with more land cover and there was moderate indication that it was related to a higher proportion of fish and a specialized diet (Table 2, Figure 2, Table S4). Brood size was larger in territories with more specialized diets and with earlier laying date but was unrelated to the proportion of land cover or the proportion of fish (Table 2, Table S5). Nestling physical condition was strongly mediated by diet, with nestlings fed on a diet containing a high proportion of one prey type being in better physical condition than those on a diverse diet (Table 2, Figure 2, Table S6), but physical condition was unrelated to the proportion of fish in diet or land cover in the territory (Table 2, Table S6). Full model outputs can be found in Tables S3–S6.

4 | DISCUSSION

Our results indicated that in a generalist bird of prey, early-life diet was associated with offspring quality and breeding performance of the parents. However, the relationships found with diet were not the same across different breeding stages and offspring life phases: In support of the 'balanced diet hypothesis', nestlings that grew up under conditions related to parents feeding a diverse diet to their young, showed higher apparent annual survival rates. Contrary to this, the short-term fitness associations supported the 'specialized diet hypothesis': Brood sizes were larger, and nestling's physical condition was better when eagles grew up under conditions in which parents supplied narrow diets. Supporting the 'prey type hypothesis', breeding success was positively associated with a diet that was rich in fish and low in bird prey or in territories that were located in more land-based locations. This fish-rich diet was however associated with strong negative carry-over associations into an eagle's adult life in terms of apparent survival.

4.1 | A diverse early-life diet and long-term survival

In the white-tailed eagle, conditions related to a diverse early-life diet were beneficial in terms of annual survival rates. This

TABLE 1 Top 5 Cormack-Jolly-Seber (CJS) models of annual survival probability of 574 nestlings ringed between 2003 and 2014 and were recorded until 2021. Model containing proportion of fish as an explanatory variable performed better than the null model (best null model, which does not contain any explanatory variables: Φ (brood size + sex + age) has a ΔAICc = 16.93). K is the number of parameters in the model, ω_i model weight. Φ = survival probability, diet breadth = Levins' index, brood size = factor variable 1–3, sex = factor, male and female, age = year 0–5: immature, year 5 or older: adult. Resighting probability (ρ) was set as age, sex, time, and trap dependency state ('trap aware' or 'trap unaware', time-varying).

Model	AICc	ΔAICc	ω_i	K	$-2\ln l$
Φ (fish × age + diet breadth + sex + brood size)	3017.749	0.00	0.352	29	2959.517
Φ (fish × age + diet breadth + brood size)	3018.366	0.62	0.257	28	2962.149
Φ (fish × age + diet breadth + sex)	3019.18	1.44	0.169	27	2964.986
Φ (fish × age + diet breadth)	3019.504	1.76	0.143	26	2967.317
Φ (fish × age + brood size + sex)	3023.00	5.25	0.025	28	2966.781

FIGURE 1 Cormack-Jolly-Seber (CJS) effect sizes (solid lines), and 95% confidence intervals (dashed lines) of annual apparent survival probability in relation to (a) proportion of fish and age (immature, age 0–4, and adult, age 5+ years) and (b) diet breadth (Levin's index) of white-tailed eagles that were ringed as nestlings between 2003 and 2014 on the Åland Islands and resighted until 2021. Resighting probability (ρ) was modelled by sex, age, time and trap dependency.
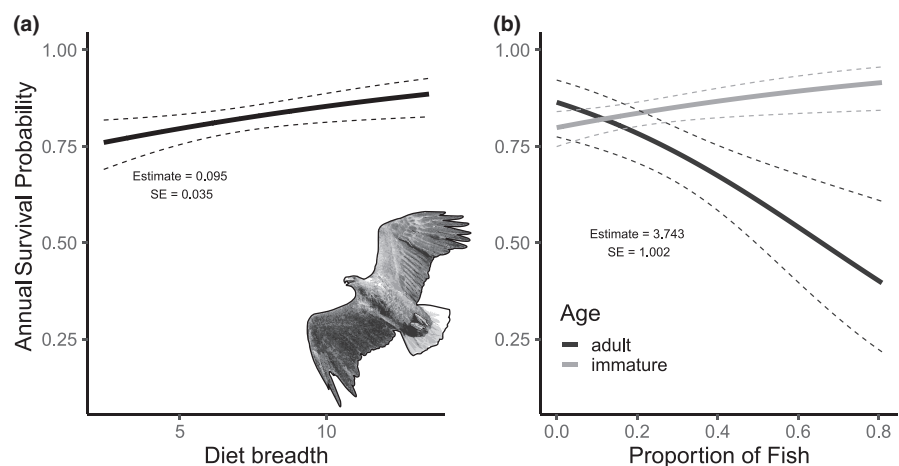
TABLE 2 Results of models explaining breeding and offspring quality parameters of white-tailed eagles. Key explanatory variables—diet breadth (Levins' index), proportion of fish (fish, %), and proportion of land area (land cover) are presented for (a) the 'timing of breeding' model, (b) 'breeding success model', (c) 'productivity model' (brood size 1 = 0; brood size 2 and 3 = 1) and (d) 'physical condition model'. While variables diet breadth and fish were fit in the same model, land cover was fit in a separate model due to high correlation with fish. Column '*N*' refers to sample size, 'year' to the collection years, model structure the GLMM family, 'co-variates' to the fitted fixed effects, 'random effects' to the random terms, column 'ndf' to the degrees of freedom of the numerator of the model. In the timing of breeding model, the breeding success model, and the productivity model, year and territory ID were added as crossed random effects. In the productivity model, we controlled for lay date by fitting the Julian day of the first hatch within the brood. In the 'physical condition model', we controlled for wing length (L = linear, Q = quadratic), sex (factor, male or female), brood size (factor, 1–3), and Julian day of hatching and 'year' and 'territory ID' as a nested random term. Full model outputs can be found in the supplementary material. All numeric variables were scaled. Statistically significant explanatory variables are highlighted in bold.

| Years	N	Model structure	Co-variates	Random effects	ndf	Variables of interest	Estimate	SE	χ^2	p
(a) Timing of breeding										
2003–2014	434	Gaussian	—	Year, territory ID (crossed)	2	**Fish**	**0.273**	**0.074**	**13.41**	**<0.001**
						Diet breadth	**0.134**	**0.052**	**6.57**	**0.010**
					1	**Land cover**[a]	**1.029**	**0.102**	**5.94**	**0.015**
(b) Breeding success										
1976–2020	1503	Binomial	—	Year, territory ID (crossed)	2	**Fish**	**0.273**	**0.074**	**13.41**	**<0.001**
						Diet breadth	−0.057	0.069	0.67	0.412
					1	**Land cover**[a]	**0.190**	**0.078**	**5.94**	**0.015**
(c) Productivity										
2003–2014	431	Binomial	Lay date	Year, territory ID (crossed)	3	Fish	0.158	0.110	2.08	0.149
						Diet breadth	**−0.284**	**0.105**	**7.30**	**0.007**
					2	Land cover[a]	−0.098	0.111	0.78	0.376
(d) Physical condition										
2003–2014	187	Gaussian	Wing length L & Q, sex, brood size, lay date	Year, territory ID (nested)	8	Fish	−0.029	0.035	0.69	0.405
						Diet breadth	**−0.107**	**0.034**	**10.0**	**0.002**
					7	Land cover[a]	−0.037	0.035	1.09	0.296

[a]Fitted in separate models to proportion of fish and diet breadth.

relationship could be caused directly by diet, as a high diversity in prey fed to nestlings might have the benefit of reducing the overall effect of environmental toxins or of enhancing the supply of nutrients (Simpson & Raubenheimer, 2012). Beneficial effects of a diverse diet might already begin during the formation of the egg if the female has similar prey available during courtship, thus leading to optimized embryonic and post-hatching development of young (Kyneb & Toft, 2006). On the one hand, if a specialized diet is associated with a higher accumulation of environmental toxins, negative long-lasting consequences on survival could be associated with impairment of nestling development (i.e. Ulbrich & Stahlmann, 2004; Winder, 1993). On the other hand, if a diverse diet is associated with optimized macro- and micronutrient supply, long-lasting benefits could be derived through optimal development of young. There is a strong mechanistic link already established between nutrition and physiological development in humans and non-carnivorous species (i.e. Kitaysky et al., 2006; Pahwa & Sharan, 2022; Swaggerty et al., 2019). Such a mechanistic link of early-life diet and apparent survival is less well understood for carnivores but might similarly be related to improved physiological development (Simpson & Raubenheimer, 2012). Indication for such comes from a field experiment in which Eurasian kestrel *Falco tinnunculus* nestlings showed

a stronger immune response if they were fed a more diverse diet (Navarro-López et al., 2014). As a well-developed immune system is also a good predictor of survival (Hegemann et al., 2013, 2015; Wilcoxen et al., 2010), this could likewise provide a potential explanation for a mechanistic link of early-life diet and apparent survival for the white-tailed eagle.

At the same time, the relationship between a diverse early-life diet and survival could be caused by the environmental conditions the nestlings experience: A more diverse early-life diet likely reflects more diverse availability of prey in the natal environment, in which post-fledging juveniles might be able to gain experience with a wider prey spectrum. In passerine birds, it has been experimentally shown that rearing diet profoundly shapes lifetime niche preferences (Slagsvold & Wiebe, 2011). The development of a large dietary niche during early life might allow young eagles to show a larger behavioural plasticity as adults and reduce the likelihood of starvation when preferred prey is scarce. The benefit of a diverse early-life diet might thus impact multiple early life stages in the white-tailed eagle and translate into the observed long-lasting positive associations with fitness. Alternatively, high quality parents might be more capable of exploiting all available resources. In that case, the observed high apparent survival of their progeny would be the result of
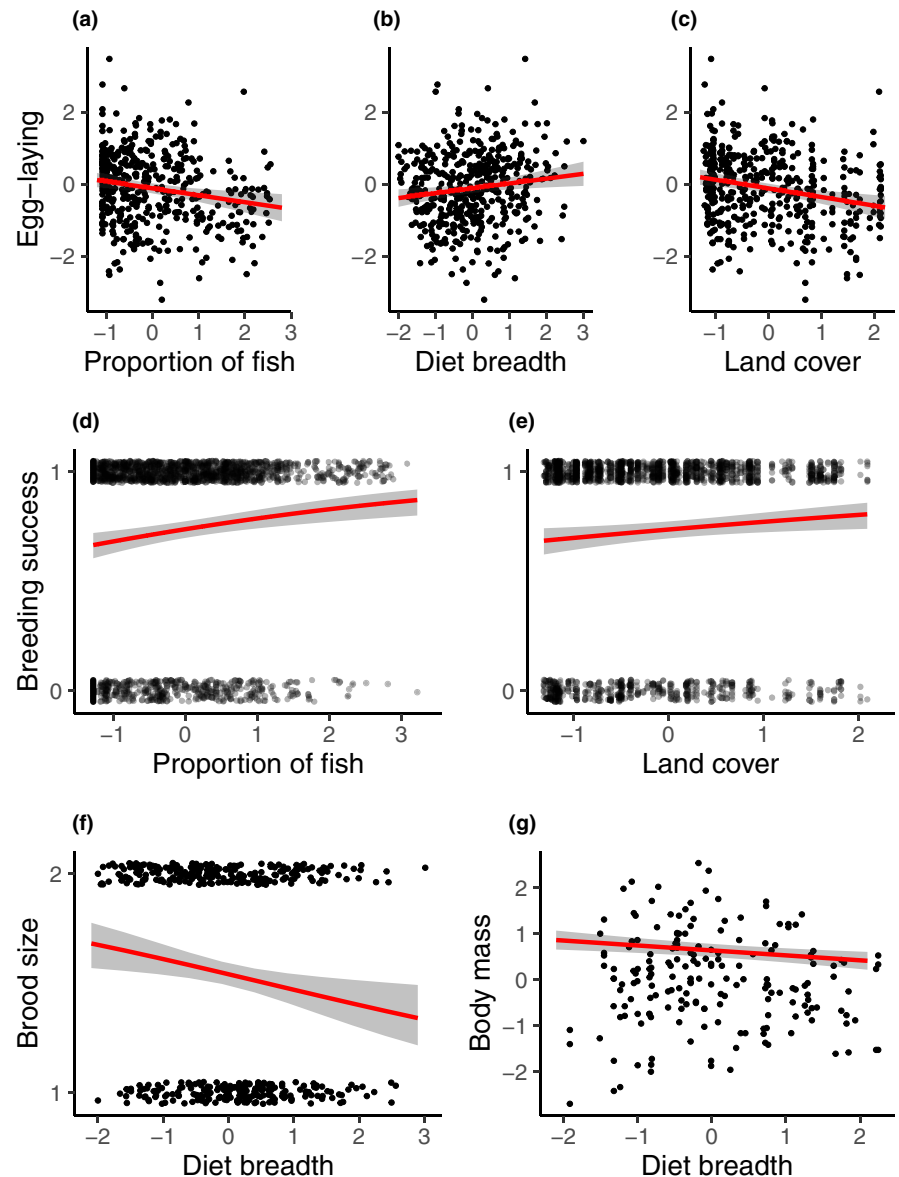
high-quality adults raising high quality offspring and be unrelated to a benefit derived through diet.

A difficulty with apparent survival is disentangling permanent emigration from mortality (Newton et al., 2016). Individuals in good condition might be more likely to emigrate than those in lower condition (Cam et al., 2003; Tilgar et al., 2010), thus explaining the contrasting relationships between short- and long-term associations. We could not control for the amount of food delivered to the nestlings in the full data, but with a subset of the data we could see that diet breadth was a better predictor of survival than the physical condition of the nestlings (an indicator of amount of food). This indicated that conditions associated with a larger diet breadth are driving the results and not conditions associated with the amount of food. That physical condition did not affect apparent survival also makes it unlikely that any of the results are explained by physical condition-dependent dispersal/emigration (e.g. Cam et al., 2003; Tilgar et al., 2010), but due to the general difficulty of

measuring physical condition in the field, especially through point-measures (García-Berthou, 2001), this remained inconclusive.

4.2 | Fish-specific diet decreases adult survival

Adult eagles that were raised on a diet that is rich in fish and low in bird prey had reduced apparent survival rates in comparison to conspecifics that were raised on a diet that was poor in fish. This relationship could arise via different pathways. On the one hand, it could arise via a behavioural pathway if rearing diet results in the formation of a foraging niche preference (Slagsvold & Wiebe, 2011), as it will then likely also affect settlement decisions. White-tailed eagles might primarily choose their breeding environment by key features and characteristics (like prey availability) that match their natal habitat. Fish-rich territories are primarily located on the Åland Island mainland, making it potentially more likely that eagles feed on mammal carcasses shot

during the autumn or winter hunting season, thus increasing risk of lead poisoning (Isomursu et al., 2018; Nadjafzadeh et al., 2013). If fish-rich territories are associated with better quality habitats (indicated by higher breeding success, discussed below), higher competition for those sites might also lead to lower survival rates in adults. As an alternative explanation, white-tailed eagles that continue to primarily feed on fish, might be more likely to bioaccumulate environmental toxins (Ekblad et al., 2021), which might only reach lethal concentrations when the eagles are older. Some environmental toxins can also have long-lasting consequences, even if exposure is limited (e.g. Bertazzi et al., 2001; Hoyeck et al., 2020; Tsukimori et al., 2008).

On the other hand, high apparent survival could be affected via a nutritional pathway: Pike is low in fat, whereas waterfowl is high in fat, especially female ducks during the breeding season (Jankowska et al., 2008; Milne, 1976). The importance of a single macronutrient like fat has been shown to be important for carnivores (Hewson-Hughes et al., 2013; Margalida, 2008) and can affect brain development in young and their learning capabilities as adults (Kitaysky et al., 2006). A high-fat diet derived from a diet high in waterfowl prey could affect white-tailed eagles in a similar fashion, although it is unclear why such neurological differences should only manifest themselves in breeding-age white-tailed eagles. *Haliaeetus* eagles have evolved as well-adapted fish-eaters and they even seem to preferably select pike (Nadjafzadeh et al., 2015; Virbickas et al., 2021), which is very low in fat. This makes a nutritional explanation questionable (but see Kitaysky et al. (2006) in which low-fat fish diets resulted in poor development of young and low adult recruitment rates in kittiwakes *Rissa tridactyla*).

Beside the associations of the diet variables of interest, there were also effects of brood size and age on apparent survival. Apparent survival rates were in similar ranges to those from other studies, but seemed to be at the lower end spectrum, especially for adult eagles (Korsman et al., 2012). In comparison to estimates from the same population from the 1990s (juvenile survival = 0.82–0.99), survival of immatures remained at similar levels (Saurola et al., 2003). Breeding age white-tailed eagles had lower apparent survival rates than their immature conspecifics, which had also been reported by Saurola et al. (2003), and might be explained by higher mortality due to territorial dispute (Saurola et al., 2003). Nestlings from larger broods had lower survival rates, indicating lower fledgling success or higher post-fledging mortality due to sharing resources or sibling competition (e.g. Neuenschwander et al., 2003; Roulin et al., 1999; but see Costantini et al., 2009).

4.3 | Associations between nestling diet and short-term breeding parameters

Territories that were more land-based or were associated with more fish prey had higher breeding success on the Åland Islands. Breeding success is quite a crude measurement, which does not distinguish between breeding failure during the courtship, incubation or early nestling stage. The found association between habitat, diet and breeding success should be viewed in a wider temporal and spatial context: eagles that primarily feed on waterfowl during the breeding season inhabit the outer archipelago of the Åland Islands, which might yield fewer prey options during winter and early spring. These habitats might also be subject to overall harsher conditions. Eagles nesting in the outer archipelago also initiated egg-laying later and the higher breeding success in the inner archipelago might be due to additive effects of habitat, timing of breeding and diet. Unfortunately, initiation of egg-laying could not be accounted for in the breeding success model as this data is unavailable for breeding attempts that failed to produce nestlings at ringing age. These results imply that territories that have access to fish-rich waters but are also land-based and potentially sheltered against harsh conditions are of highest quality for white-tailed eagles. If these territories are subject to strongest competition, they will be occupied by highest quality adults, which might indirectly explain the association of diet and habitat with earlier initiation of breeding and higher breeding success (Sergio et al., 2007).

During the nestling period, conditions related to a general diet specificity were associated with differences in brood size and the physical condition of nestlings. Those two parameters are tightly associated with each other as nestlings in better physical condition are less likely to die. This result indicates that specialized fish- and bird-diets result in equal amounts of energy available, a common explanation for higher breeding success in other bird of prey species (Katzner et al., 2005; Llorente-Llurba, 2019; but see Margalida et al., 2009; Whitfield et al., 2009). For future research, it would be interesting to investigate the calorie content of individual prey species and whether waterfowl prey is harder to catch than fish (Nadjafzadeh et al., 2016) but energetically more valuable due to higher fat content.

4.4 | Conclusion

We show that early-life diet might shape long-term fitness in a wild bird of prey. (1) Conditions related to a large early-life diet breadth resulted in beneficial long-term fitness (measured as annual apparent survival). This result indicates that young receive a developmental benefit from growing up under more diverse conditions, potentially either directly through their diet (Navarro-López et al., 2014; Simpson & Raubenheimer, 2012) or from the more varied experiences they make in their natal environment (English et al., 2016). (2) Early-life conditions and prey type were related to differences in apparent survival in adult life, indicating that either a specific diet is associated with contaminant accumulation (HELCOM, 2010) or that settlement decisions are shaped by natal environment characteristics. (3) Although the mechanisms shaping the short- and long-term associations with diet are unclear at this point, our results reveal potentially important parent-offspring strategies. On the one hand, parents might fare better and raise more young if they live in an environment where they can specialize on one or a few types of prey. On the other hand, those young are potentially less competitive towards their conspecifics and

fare worse in terms of their apparent survival. Whether this leads to overall higher success of generalist or specialist individuals and their progeny within the population over time would be interesting to explore further.

Studies on early-life diet and their long-lasting fitness consequences for predators are surprisingly limited in the published literature. This is especially true for large birds of prey. Patterns found in this study might be widespread in other carnivorous species. Long-lasting associations of nestling diet could have the potential to shape eco-evolutionary dynamics within species and even have large scale implications for wild predator populations (see i.e. Kitaysky et al., 2006). As many carnivorous species are also endangered, our results might have direct implications for carnivore and predator conservation. However, more in-depth studies are needed to determine and disentangle the mechanistic relationships that could explain how early-life conditions translate into observed long-lasting fitness consequences in wild predators.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: DNA extraction and genotyping lab procedure.