BMC Biology

RESEARCH

Open Access

Sibling cooperation in boreal owls during the post-fledging dependence period

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Abstract

Background Many vertebrates develop in the company of their siblings, a social context that profoundly influences their life histories and phenotypes. While avian begging behaviour in parent–offspring conflict and sibling competition/cooperation have been largely studied in nestlings, the fledglings' begging remains under-researched, despite the continued dependency of young birds throughout the post-fledging dependence period (PFDP). Siblings typically maintain close proximity during the PFDP, a pattern that might be explained by the following four mutually non-exclusive hypotheses: competition over the prey delivered by parents (competition, H1), mutual affection established during the nestling period (cooperation-friendship, H2), various antipredation behaviours (cooperation-antipredation, H3) or begging negotiation about whose need is greater (cooperation-negotiation, H4).

Results We radio-tracked 123 boreal owl (*Aegolius funereus*) fledglings from 34 nests over 6 years in Czechia and Finland and recorded daily inter-sibling distances throughout the PFDP. Distances were longer in Czechia than in Finland during both night (82 ± 81 vs 56 ± 65 m; mean ± SD) and day (75 ± 109 vs 64 ± 86 m). In both areas, distances increased with an augmenting time gap in tracking, siblings' age and the number of present siblings at night but decreased during the day. These consistent patterns across different environments indicate that the life history of the target species prevails over the environmental effects. Consistent with the predictions of the cooperation-antipredation hypothesis (H3), the mean inter-sibling distances were shorter in Finland compared to Czechia during both day and night, and inter-sibling distances were shorter within larger sibling flocks during the day. The cooperation-negotiation hypothesis (H4) is supported by the finding that vocally begging siblings were closer to each other than their non-begging counterparts.

Conclusions Our results demonstrate, for the first time, that sibling cooperation can occur during the PFDP, when offspring are vulnerable to predators, both during diurnal roosting and at night while begging for food. We conclude that the inter-sibling distances in boreal owls during the PFDP are maintained because siblings cooperate through collective antipredation behaviour during diurnal roosting and through collective negotiation over access to the indivisible prey items delivered by their parent during nocturnal activity.

Keywords Altruistic behaviour, Anti-predation behaviour, Begging behaviour, Birds of prey, Selfish behaviour, Hatching asynchrony, Radio-telemetry, Relatedness, Sibling competition, Sibling negotiation

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Background

Many vertebrates grow up in the company of same-age or different-age siblings, and relations among them can be expected to significantly influence individual life histories and the development of individual morphological, physiological and behavioural phenotypes [1, 2]. Shared spatiotemporal environmental conditions are decisive for issues arising from parent–offspring conflict and sibling competition and/or cooperation (e.g., [2–5]). The conditions that siblings share and their mutual interactions can differ markedly across taxa and various stages of ontogeny during the offspring's dependency period. For instance, in mammals, the stages of being in utero [6], suckling bouts after delivery [7], at weaning in carnivores when parents start to bring solid food [8], and in birds during the nestling phase [9, 10] and the post-fledging dependence period (PFDP hereinafter) [11] are barely comparable.

Interactions among siblings range from direct competition to sophisticated cooperation. Siblings usually compete over limited food resources, which may even result in siblicide in some species (reviewed by [1]). Cooperation among siblings may increase food delivery by their parents through intensified vocal begging [12, 13] or save energy through joint thermoregulation, i.e. sharing the burden of heat production [12, 14]. Begging negotiation about who has the greater need and who will receive the next indivisible prey item may reduce the cost of sibling competition for parental attention [9, 15, 16]. Therefore, the range of mutual sibling behaviour/interactions can be vast and temporally variable, and it is always the stronger/older siblings that determine whether within-brood relationships are described as parasitism, mutualism or commensalism [12]. Whatever form of inter-sibling relation is being observed, it must be evaluated and examined in terms of the inclusive fitness of the observed individuals [17].

Most theoretical and empirical studies of avian begging behaviour in parent–offspring conflict and sibling competition/cooperation have focused on nestlings (e.g., [18–21]). In contrast, due to the technical difficulty of collecting this data, studies on begging by fledglings are scarce, despite young birds continuing to beg long after nest departure, typically until the end of the PFDP. For instance, Middleton et al. [22] found that fledglings of American dippers (*Cinclus mexicanus*) begged at higher intensities in a year with lower food abundance and observed reduced parental provisioning rates during this year, suggesting that begging may reflect long-term condition and need. Fledglings of the pied babbler (*Turdoides bicolor*) revealed their need by moving to a riskier location [23]. They thus were able to manipulate adults into achieving higher provisioning rates. Therefore, as in the case of offspring positioning themselves at different sides of open cup nests, which may be connected with the preferred side for feeding by male or female parent [24, 25], or staying close to or even moving directly into the entrance hole of cavity nests [26, 27], the fledged offspring spatial positioning or their inter-sibling distances may be analogous and can play various specific roles during the PFDP. However, as far as we know, there are no earlier studies on inter-sibling distances throughout the PFDP across different bird species, though studies of nestlings' positioning within the open or cavity nests waiting for food deliveries are a standard part of the field of sibling competition/cooperation studies (e.g., [24–26]).

Our model species, the boreal owl (*Aegolius funereus*), is a small, nocturnal predatory bird inhabiting the coniferous forests of the Holarctic zone [28]. Their diet consists mainly of small rodents, especially voles of the genera *Microtus* and *Myodes*, as well as alternative prey such as shrews of the genus *Sorex* and small forest birds [29, 30]. Prey abundance is crucial to boreal owls' foraging, spatial behaviour and reproduction [30–32]. The chicks hatch asynchronously at 2-day intervals; thus, in large broods, there can be up to 2 weeks' difference in age and size between offspring [27, 33, 34]. They stay in the nest for 27–38 days after hatching, usually fledge at 1-day intervals in the same order as they hatched [35], and reach independence 5–9 weeks after fledging [36].

In the boreal owl, the great majority of prey brought to the young throughout the late nestling and PFDP is delivered by the male [33, 37, 38]. We refer to "parent", but males are primarily the only caregivers. During this time, the offspring vocalise to solicit food from the parent with short, hissing *cheet* calls [28]. The begging-calling behaviour of boreal owl fledglings was studied as part of the parent–offspring conflict theory. The most important measures related to the probability of vocalisation were body condition at fledging, time of night, number of surviving siblings, age and weather conditions [11]. Begging intensity increased with age, and fledglings vocalised significantly more often in the year with low prey abundance, suggesting honest signalling of their needs [11].

Overall, many studies have already been published regarding nestlings' behaviour during their stay on the nest in the context of siblings' competition and/or cooperation across different bird taxa. However, the current study is unique because, to the best of our knowledge, no study to date has addressed inter-sibling interactions within this context and/or tested different variables to identify the factors that decisively determine siblings' relationships based on their spatiotemporal co-occurrence throughout the entire PFDP.

Our study aimed to explore factors that may influence the distance between siblings in boreal owl fledglings, including environmental variables, time of day and individual siblings' characteristics, such as age, across two geographically and environmentally distinct locations:

Table 1 Basic breeding data. Basic breeding data for the nests in which at least two nestlings were equipped with radio transmitters, successfully fledged from, and monitored during the post-fledging dependence period within the six study years. The number of monitored nests and mean numbers (± standard deviations) and ranges of clutch sizes, hatchlings, fledglings, their sex, radio-tracked and dispersed individuals, dates of nesting, hatching, fledging and dispersing, duration of nestling period, recorded inter-sibling distances during nocturnal activity and diurnal roosting and spring prey abundance determined by snap-trapping and listed as the number of trapped individuals (small mammals) per 100 trap nights recorded within the two study sites in Czechia and Finland are provided

	Mean ± SD	**Min–Max**	**Mean ± SD**	**Min–Max**
Year	2010–2012, 2015		2019, 2021	
Country (study area)	Czech Republic (Ore Mts.)		Finland (Kauhava)	
Area size (square km)	120		1000	
No. of involved nests[1]	16		18	
Clutch size	6.1 ± 1.3	4–8	6.0 ± 1.0	4–7
No. of hatchlings	5.4 ± 1.7	2–8	5.8 ± 1.1	4–7
No. of fledglings	4.8 ± 1.8	2–8	3.0 ± 1.3	2–6
Sex of fledglings (M: F)	34: 35		32: 22	
No. of radio-tracked fledglings	69		54	
No. of dispersed fledglings	3.4 ± 1.5	1–6	1.8 ± 1.7	0–5
Sum of dispersed individuals	55		32	
Date of nesting (± days)	26 March ± 9	13 March–16 April	3 April ± 14	19 March–3 May
Date of hatching (± days)	28 April ± 9	10 April–22 May	5 May ± 15	16 April–4 June
Date of fledging (± days)	30 May ± 9	11 May–22 June	7 June ± 14	19 May–5 July
Date of reaching independence (± days)	18 July ± 9	1 July–3 August	21 July ± 10	3 July–11 August
Duration of nestling period (days)	32 ± 2	27–38	32 ± 3	27–40
No. of night inter-sibling distances	2131		1145	
No. of day inter-sibling distances	2619		1185	
Prey abundance (spring)[2]	10.19; 0.55; 4.87; 2.50		0.42; 7.80	

[1] Each nest with two or more fledged individuals

[2] Prey abundances in particular study seasons (number of individuals per 100 trap nights), respectively

Czechia and Finland (see details on both study areas below). We set up four alternative hypotheses that may explain the reasons for maintaining certain inter-sibling distances in boreal owls during the PFDP. We predicted that inter-sibling distances are maintained short because they compete for the prey items delivered by their parent, as suggested by the Competition Hypothesis (H1), or one of the three following types of cooperation. The Cooperation – Friendship Hypothesis (H2) suggests that the distances are maintained due to mutual affection, a "friendship", established in the nest during the nestling period. According to the Cooperation – Antipredation Hypothesis (H3), sibling distances are based on a set of antipredation behaviours and reflect differences in predation risk and its causes between Czechia and Finland. Finally, the Cooperation – Negotiation Hypothesis (H4) predicts that during the Night, the begging negotiation between siblings about whose need is greater, *sensu* [9], will affect inter-individual distances. The detailed reasoning for each main hypothesis (H1–H4) and their corresponding sub-hypotheses (a–k), allowing for confirmation or rejection of the main hypotheses, is provided at the beginning of the Methods section below.

Results

We monitored 34 nests from which at least two siblings fledged, resulting in 69 and 54 fledglings from 16 nests during four breeding seasons in Czechia and 18 nests during two seasons in Finland, respectively. There were 4.8 ± 1.8 (mean ± SD) fledged siblings in the Czech study area, and 3.0 ± 1.3 in the Finnish study area (breeding data are in Table 1).

During the post-fledging phases, we recorded 7080 individual inter-sibling distances (4750 in Czechia and 2330 in Finland) (Table 1). The mean distance between Czech siblings was 26 m longer during the night and 11 m longer during the day than between Finnish siblings (Table 2). The inter-sibling distances between night and day varied over time within and between the two study sites (see the results for models I–IV and the specific fixed effects tested in Tables 3 and 4 below). Within study sites, the inter-sibling distances tended to be longer at

Table 2 List of explanatory variables used. Individual fixed effects tested for their association with the dependent variable, the inter-sibling distances of boreal owl fledglings recorded throughout the post-fledging dependence period (or nocturnal activity only) in the study area of Czechia (models I and III) and Finland (models II and IV). Fixed effects for the nocturnal activity (Night) and diurnal roosting (Day), and their units, ranges (minimum–maximum), and means ± standard deviations, including an explanation of each variable, are provided

Numerical fixed effects	Unit	Czechia—nocturnal activity ($n = 2131$)		Czechia—diurnal roosting ($n = 2619$)		Finland—nocturnal activity ($n = 1145$)		Finland—diurnal roosting ($n = 1185$)	
		Mean ± SD	Min–Max	Mean ± SD	Min–Max	Mean ± SD	Min–Max	Mean ± SD	Min–Max
Hatching date: mean date of hatching of two particular siblings (1 = 1st April)	Date (day)	24 ± 9	11–52	24 ± 10	11–52	43 ± 15	18–64	43 ± 15	17–64
Siblings' age from hatching: mean age in days from hatching of two particular siblings	Day	53 ± 13	30–92	56 ± 14	30–93	49 ± 11	28–83	49 ± 11	28–82
Siblings' age difference: number of days between hatching one sibling and the other sibling	Day	5 ± 3	1–14	4 ± 2	1–14	4 ± 2	2–10	4 ± 2	2–10
No. of present siblings: daily actual number of present, live and on parents still dependent siblings outside the nest box	Number	5 ± 1	2–7	4 ± 1	2–7	4 ± 1	2–5	4 ± 1	2–5
Tracking time[1]: mean day or night time of finding two particular siblings	hh:mm	23:55 ± 1.1 h	22:01–3:52	14:29 ± 2.9 h	7:07–20:15	0:43 ± 0.9 h	22:58–3:36	14:15 ± 2.3 h	8:38–20:08
Time gap in tracking: time in minutes between finding one sibling and the other sibling	Minute	12.4 ± 13.4	1–157	9.7 ± 8.7	0–92	7.9 ± 8.2	0–88	8.2 ± 9.1	0–96
Daily precipitation: total amount of precipitation during the given day of tracking the siblings	Milimeter	2.8 ± 6.7	0–62.0	3.4 ± 7.0	0–43.2	0.9 ± 2.7	0–13.4	1.1 ± 3.1	0–15.7
Prey abundance (spring): number of captured small mammals per 100 trap nights during study breeding seasons	inds./100 t-n	6.90 ± 3.25	0.55–10.19	3.54 ± 1.59	2.50–4.87	7.23 ± 1.97	0.42–7.8	7.31 ± 1.83	0.42–7.8
Categorical fixed effects									
Sex of siblings: possible categories of sex combination of two particular siblings	Classes, $n = 3$ levels	male-male = MM, male–female = MF, female-female = FF							
Begging calling: possible categories based on the presence/absence of begging calling of two siblings in a given pair	Classes, $n = 3$ levels	yes-yes = YY, yes–no = YN, no–no = NN							
Dependent variable									
Inter-sibling distance: the direct distance between two particular siblings	Meter	82 ± 81	0–743	75 ± 109	0–802	56 ± 65	0–600	64 ± 86	0–626

[1] Tracking time was tested during exploratory analysis, but was not influential. Kept here for descriptive and informative reasons

Table 3 Composition of the best models. Composition (applied fixed effects) of the five best-fitting models sorted according to fitting statistics AIC (the smaller, the better), ΔAIC, AIC weights and AIC odds, including the Null model (AIC and relative information loss) for the modelled dependent variable (models I–IV)

Model No.[1]	AIC	Δ AIC	AIC weights wi	AIC Odds
Model (I)—Fledged siblings' distances during the PFDP in Czechia				
1) Time gap in tracking(day/night), siblings' age from hatching(day/night), No. of present siblings(day/night), siblings' age difference(day/night), sex of siblings(day/night)	54,916.91	0.00	0.99	1.00
2) Time gap in tracking(day/night), siblings' age from hatching(day/night), No. of present siblings(day/night), siblings' age difference(day/night), daily precipitation(day/night)	54,925.40	8.49	0.01	69.68
3) Time gap in tracking(day/night), siblings' age from hatching(day/night), daily precipitation(day/night), prey abundance(day/night), sex of siblings(day/night)	54,984.28	67.37	0.00	4.27E + 14
4) Time gap in tracking(day/night), siblings' age from hatching(day/night), siblings' age difference(day/night), hatching date(day/night), sex of siblings(day/night)	55,010.90	93.99	0.00	2.57E + 20
5) Time gap in tracking(day/night), siblings' age from hatching(day/night), siblings' age difference(day/night), hatching date(day/night), daily precipitation(day/night)	55,101.23	184.32	0.00	1.06E + 40
Null model	56,975.67	2058.76	0.00	-
Relative information loss to the best model (No. 1)	0.00E + 00	-	-	-
Model (II)—Fledged siblings' distances during the PFDP in Finland				
1) Time gap in tracking(day/night), siblings' age from hatching(day/night), No. of present siblings(day/night), siblings' age difference(day/night), sex of siblings(day/night)	26,134.07	0.00	1.00	1.00
2) Time gap in tracking(day/night), siblings' age from hatching(day/night), siblings' age difference(day/night), hatching date(day/night), sex of siblings(day/night)	26,149.21	15.14	0.00	1934.81
3) Time gap in tracking(day/night), siblings' age from hatching(day/night), daily precipitation(day/night), prey abundance(day/night), sex of siblings(day/night)	26,157.54	23.47	0.00	1.25E + 05
4) Time gap in tracking(day/night), siblings' age from hatching(day/night), No. of present siblings(day/night), siblings' age difference(day/night), daily precipitation(day/night)	26,161.80	27.73	0.00	1.05E + 06
5) Time gap in tracking(day/night), siblings' age from hatching(day/night), siblings' age difference(day/night), prey abundance(day/night), hatching date(day/night)	26,178.60	44.53	0.00	4.66E + 09
Null model	26,847.91	713.84	0.00	-
Relative information loss to the best model (No. 1)	9.81E − 156	-	-	-
Model (III)—Fledged siblings' distances during nocturnal activity in Czechia				
1) Time gap in tracking, siblings' age from hatching, No. of present siblings, siblings' age difference, sex of siblings, begging calling	24,303.79	0.00	0.61	1.00
2) Time gap in tracking, siblings' age from hatching, No. of present siblings, sex of siblings, begging calling	24,304.70	0.91	0.39	1.58
3) Time gap in tracking, siblings' age from hatching, daily precipitation, prey abundance, sex of siblings, begging calling	24,317.09	13.30	0.00	769.51
4) Time gap in tracking, siblings' age from hatching, siblings' age difference, hatching date, sex of siblings, begging calling	24,317.56	13.77	0.00	974.39
5) Time gap in tracking, siblings' age from hatching, siblings' age difference, hatching date, begging calling	24,318.58	14.79	0.00	1622.86
Null model	24,794.66	490.87	0.00	-
Relative information loss to the best model (No. 1)	2.57E-107	-	-	-
Model (IV)—Fledged siblings' distances during nocturnal activity in Finland				
1) Time gap in tracking, siblings' age from hatching, No. of present siblings, siblings' age difference, sex of siblings, begging calling	12,480.88	0.00	0.87	1.00
2) Time gap in tracking, siblings' age from hatching, No. of present siblings, sex of siblings, begging calling	12,484.92	4.04	0.12	7.50
3) Time gap in tracking, siblings' age from hatching, daily precipitation, siblings' age difference, No. of present siblings, begging calling	12,491.37	10.49	0.00	189.26
4) Time gap in tracking, siblings' age from hatching, daily precipitation, prey abundance, sex of siblings, begging calling	12,492.36	11.48	0.00	310.74
5) Time gap in tracking, siblings' age from hatching, siblings' age difference, No. of present siblings, begging calling	12,493.37	12.49	0.00	515.15
Null model	12,822.01	341.13	0.00	-
Relative information loss to the best model (No. 1)	8.42E − 75	-	-	-

[1] All fixed effects in the first two models (I, II) were nested within the daytime period (day/night)

Table 4 Model information. Estimate (β), standard error (SE) and 95% confidence interval (CI) of the fixed factors in the "best" models of the modelled dependent variable (models I–IV). Variables with 95% CI that do not cross zero are shown in bold text

Model[1]	Model No	Effect	Estimate	SE	95% CI	
Model (I)—Fledged siblings' distances during the PFDP in Czechia	1)	**Time gap in tracking (day)**	**6.37**	**0.18**	**6.02**	**6.73**
		Time gap in tracking (night)	**1.96**	**0.13**	**1.70**	**2.23**
		Siblings' age from hatching (day)	**2.48**	**0.11**	**2.27**	**2.70**
		Siblings' age from hatching (night)	**1.36**	**0.14**	**1.10**	**1.63**
		No. of present siblings (day)	**− 23.25**	**2.69**	**− 28.52**	**− 17.97**
		No. of present siblings (night)	**4.51**	**2.03**	**0.50**	**8.51**
		Siblings' age difference (day)	0.63	0.74	− 0.81	2.08
		Siblings' age difference (night)	0.09	0.66	− 1.20	1.38
		Sex of siblings FF (day)[2]	6.63	18.72	− 30.08	43.34
		Sex of siblings MF (day)[2]	7.22	18.54	− 29.15	43.59
		Sex of siblings MM (day)[2]	16.89	18.85	− 20.09	53.86
		Sex of siblings FF (night)	− 10.15	6.15	− 22.22	1.93
		Sex of siblings MF (night)	1.05	4.97	− 8.69	10.79
		Sex of siblings MM (night)	0.00	-	-	-
Model (II)—Fledged siblings' distances during the PFDP in Finland	1)	**Time gap in tracking (day)**	**4.07**	**0.22**	**3.65**	**4.49**
		Time gap in tracking (night)	**3.04**	**0.25**	**2.56**	**3.52**
		Siblings' age from hatching (day)	**1.82**	**0.18**	**1.46**	**2.17**
		Siblings' age from hatching (night)	**1.13**	**0.19**	**0.76**	**1.50**
		No. of present siblings (day)	**− 7.28**	**3.05**	**− 13.26**	**− 1.31**
		No. of present siblings (night)	− 0.26	3.09	− 6.32	5.79
		Siblings' age difference (day)	**4.66**	**1.03**	**2.65**	**6.67**
		Siblings' age difference (night)	0.83	1.02	− 1.18	2.84
		Sex of siblings FF (day)	− 24.21	20.08	− 63.58	15.16
		Sex of siblings MF (day)	− 25.56	19.01	− 62.84	11.73
		Sex of siblings MM (day)	− 28.75	19.12	− 66.24	8.75
		Sex of siblings FF (night)	− 8.41	7.42	− 22.95	6.14
		Sex of siblings MF (night)	− 5.98	5.20	− 16.17	4.21
		Sex of siblings MM (night)	0.00	-	-	-
Model (III)—Fledged siblings' distances during nocturnal activity in Czechia	1)	**Time gap in tracking**	**1.92**	**0.12**	**1.68**	**2.16**
		Siblings' age from hatching	**1.55**	**0.14**	**1.27**	**1.83**
		No. of present siblings	**7.39**	**2.24**	**2.99**	**11.80**
		Siblings' age difference	0.12	0.62	− 1.09	1.33
		Sex of siblings FF	− 11.63	6.10	-23.60	0.34
		Sex of siblings MF	0.80	4.84	− 8.70	10.30
		Sex of siblings MM	0.00	-	-	-
		Begging calling YY[3]	**− 21.99**	**5.52**	**− 32.82**	**− 11.15**
		Begging calling YN[3]	2.92	4.11	− 5.14	10.98
		Begging calling NN[3]	0.00	-	-	-
	2)	**Time gap in tracking**	**1.92**	**0.12**	**1.68**	**2.16**
		Siblings' age from hatching	**1.55**	**0.14**	**1.27**	**1.83**
		No. of present siblings	**7.47**	**2.20**	**3.13**	**11.80**
		Sex of siblings FF	− 11.58	6.10	− 23.54	0.38
		Sex of siblings MF	0.85	4.84	− 8.64	10.33
		Sex of siblings MM	0.00	-	-	-
		Begging calling YY	**− 22.00**	**5.52**	**− 32.82**	**− 11.17**
		Begging calling YN	2.92	4.11	− 5.14	10.97
		Begging calling NN	0.00	-	-	-

Table 4 (continued)

Model[1]	Model No	Effect	Estimate	SE	95% CI	
Model (IV)—Fledged siblings' distances during nocturnal activity in Finland	1)	**Time gap in tracking**	**3.01**	**0.21**	**2.59**	**3.43**
		Siblings' age from hatching	**1.27**	**0.18**	**0.92**	**1.62**
		No. of present siblings	**10.59**	**3.31**	**4.10**	**17.09**
		Siblings' age difference	1.40	0.90	−0.38	3.17
		Sex of siblings FF	−10.32	7.53	−25.09	4.46
		Sex of siblings MF	−3.63	4.59	−12.63	5.38
		Sex of siblings MM	0.00	-	-	-
		Begging calling YY	**−12.48**	**4.94**	**−22.18**	**−2.79**
		Begging calling YN	4.90	4.93	−4.78	14.58
		Begging calling NN	0.00	-	-	-

[1] All fixed effects in the first two models (I, II) were nested within the daytime period (day/night)

[2] Pairs of siblings according to their sex: FF (two females), MF (male and female), MM (two males)

[3] Pairs of siblings according to presence/absence of begging calls: YY (yes-yes), YN (yes–no), NN (no–no)

night than during the day in Czechia, whereas the opposite was observed in Finland. Between the study sites, the inter-sibling distances were longer at night and during the day in Czechia than in Finland (Table 2). Inter-sibling distances differed significantly between the two countries (Kruskal–Wallis test, ChiSq = 57.8, $P < 0.0001$).

The two countries differed in various environmental (see below and Additional file 1: Table S1) and behavioural aspects. Therefore, we analysed the data separately for each country using the same a priori hypotheses for the first two models (I, II; Additional file 1: Table S2), and the same a priori hypotheses (a bit different compared to the two above models) for the next two models (III, IV; Additional file 1: Table S3). Additional file 1: Table S4 (models I – IV) shows the five best candidate models ranked according to the four information criteria. They all ranked the same five GLMM models as the best; therefore, only AIC's results are presented here. The five best candidate models for the dependent variable (models I–IV), ranked by AIC, are presented in Table 3. Uniform rankings across the four information criteria provide a convincing argument that the models with cross-level interactions are the best. The relative information loss from comparing the Null and best models confirms that the best and other top-ranked models have merit (Table 3). The coefficient estimates, standard errors and 95% confidence intervals for fixed effects included in the "best" and equivalent models are shown in Table 4.

Inter-sibling distances during the PFDP in Czechia (model I)

For the dependent variable, the inter-sibling distances during the PFDP in Czechia, the Δ values of AIC (along with other information criteria; see Additional file 1: Table S4) conclusively identified one best-fitting model [39] with a probability of 99% (Table 3). The model with the second-lowest AIC value had 70 times the probability (AIC odds) of not being the best model (Table 3). Therefore, no other model should be considered.

The best model explaining the inter-sibling distances during the PFDP in Czechia included five fixed effects, each nested within the daytime period (day/night): time gap in tracking, siblings' age from hatching, number of present siblings, siblings' age difference and sex of siblings (Tables 3 and 4). The inter-sibling distances increased with the longer tracking time of two given siblings during both the Night (nocturnal activity) and Day (diurnal roosting) period (Fig. 1a), advancing siblings' age for both the Night and Day (Fig. 1c) and increasing number of present siblings during the Night but the opposite was found for the Day when the distances decreased with increasing number of siblings present (Fig. 1e). The inter-sibling distances remained unaffected by the siblings' age difference for both the Night and Day (Fig. 1g), and the sex of the two siblings in each pair during both the Night and Day (Fig. 2).

Inter-sibling distances during the PFDP in Finland (model II)

For the dependent variable, inter-sibling distances during the PFDP in Finland, the Δ values of AIC (along with other information criteria; see Additional file 1: Table S4) conclusively identified a single best-fitting model [39] with a probability of 100% (Table 3). The model with the second-lowest AIC value had a probability (AIC odds) 1935 times higher that it is not the best model (Table 3). Therefore, we did not consider any other model.

The best model explaining the inter-sibling distances during the PFDP in Finland included five fixed effects, each nested within the daytime period (day/night): time gap in tracking, siblings' age from hatching, number of present siblings, siblings' age difference and sex of siblings (Tables 3 and 4). The inter-sibling distances increased with the longer tracking time of two given siblings during both the Night (nocturnal activity) and Day (diurnal roosting) period (Fig. 1b) and advancing siblings' age for both the Night and Day (Fig. 1d). The distances further decreased with the increasing number of present siblings during the Day but only marginally during the Night (Fig. 1f). The inter-sibling distances also increased with the growing age difference between siblings during the Day but were relatively stable/unaffected during the Night (Fig. 1h). The sex of the two siblings in each pair appeared not to affect the inter-sibling distances during Night or Day (Fig. 2).

Inter-sibling distances during nocturnal activity (models III, IV)

During nocturnal activity in Czechia, an analysis of inter-sibling distances revealed two best-fitting models based on the Δ values of the Akaike Information Criterion (AIC) and other information criteria (see Additional file 1: Table S4). These models had probabilities of 61% and 39% (AIC weight) of being the best models. A weighted estimate of the predicted values, which accounted for the Akaike weights [40], indicated that the following factors were involved in both significant models: the time gap in tracking, the age of siblings from hatching, the number of present siblings, the sex of the siblings and the presence/absence of begging calls (100% involvement). Although the age difference was the only variable present only in the "best" model, it had a minor influence (as indicated by the confidence interval in Table 4). This suggests that the difference between the best and the second-best model may reflect an unintentional bias from the researcher. Therefore, the contents of the "best" model, excluding the age difference, should be considered optimal.

Regarding the analysis of inter-sibling distances during nocturnal activity in Finland, the Δ values of AIC (along with other information criteria; see Additional file 1: Table S4) nominated one best-fitting model with a probability of 87% (model IV, Table 3). The model with the second-lowest AIC value had 7.5 times the probability (AIC odds) of not being the best model (Table 3). Therefore, no other model should be considered.

The best models explaining the inter-sibling distances during nocturnal activity in Czechia (model III, Table 3) and Finland (model IV, Table 3) included the same five fixed effects which were included also in the best models I and II (each nested within daytime period "day/night") in the above analyses, i.e., time gap in tracking, siblings' age from hatching, number of present siblings, siblings' age difference and sex of siblings (Tables 3 and 4) but included also the presence/absence of begging calling which proved to be highly influential (Table 4). The inter-sibling distances between siblings that were heard producing begging calls were shorter compared to those that were silent (Fig. 3).

The graphical representations of the results for the last two models (III, IV) were very similar to those for the first two models (I, II) shown in Fig. 1, with one exception. The number of present siblings had no effect on the inter-sibling distances during nocturnal activity in Finland (model II, Fig. 1f) when analysed together with diurnal data and nested within the daytime period (day/night). However, the distances increased with the rising number of present siblings (model IV) when the nocturnal data were analysed separately (without diurnal data and nesting within the daytime period) (Fig. 4; therefore, only this result is graphically presented here). The results regarding the sex of siblings (models I and II, Fig. 2) are not repeated for the last two models (III, IV), as they were identical and non-influential in all models (Table 4).

Discussion

The inter-sibling distances of boreal owl fledglings during the PFDP were affected by the same factors, including time gap in tracking, siblings' age from hatching, number of present siblings and presence/absence of begging calling at night in both the Central and North European study areas, although their environments notably differ with respect to night length, altitude, weather conditions, habitat composition and predation risk [41–43]. Interestingly, the same factors were also influential during siblings' nocturnal activity and diurnal roosting. The fact that the same factors determined inter-sibling distances

(See figure on next page.)

Fig. 1 Inter-sibling distances recorded in Czechia and Finland. Predicted values of inter-sibling distances of boreal owl fledglings recorded throughout the post-fledging dependence period in the Czech and Finnish study area during the nocturnal activity (Night) and diurnal roosting (Day) plotted against the time gap in tracking (**a**, **b**), siblings' age from hatching (**c**, **d**), number of present siblings (**e**, **f**) and siblings' age difference (**g**, **h**) with regression lines and 95% confidence intervals. The bubble size corresponds to the number of predicted (overlapping) cases between 1 and 35

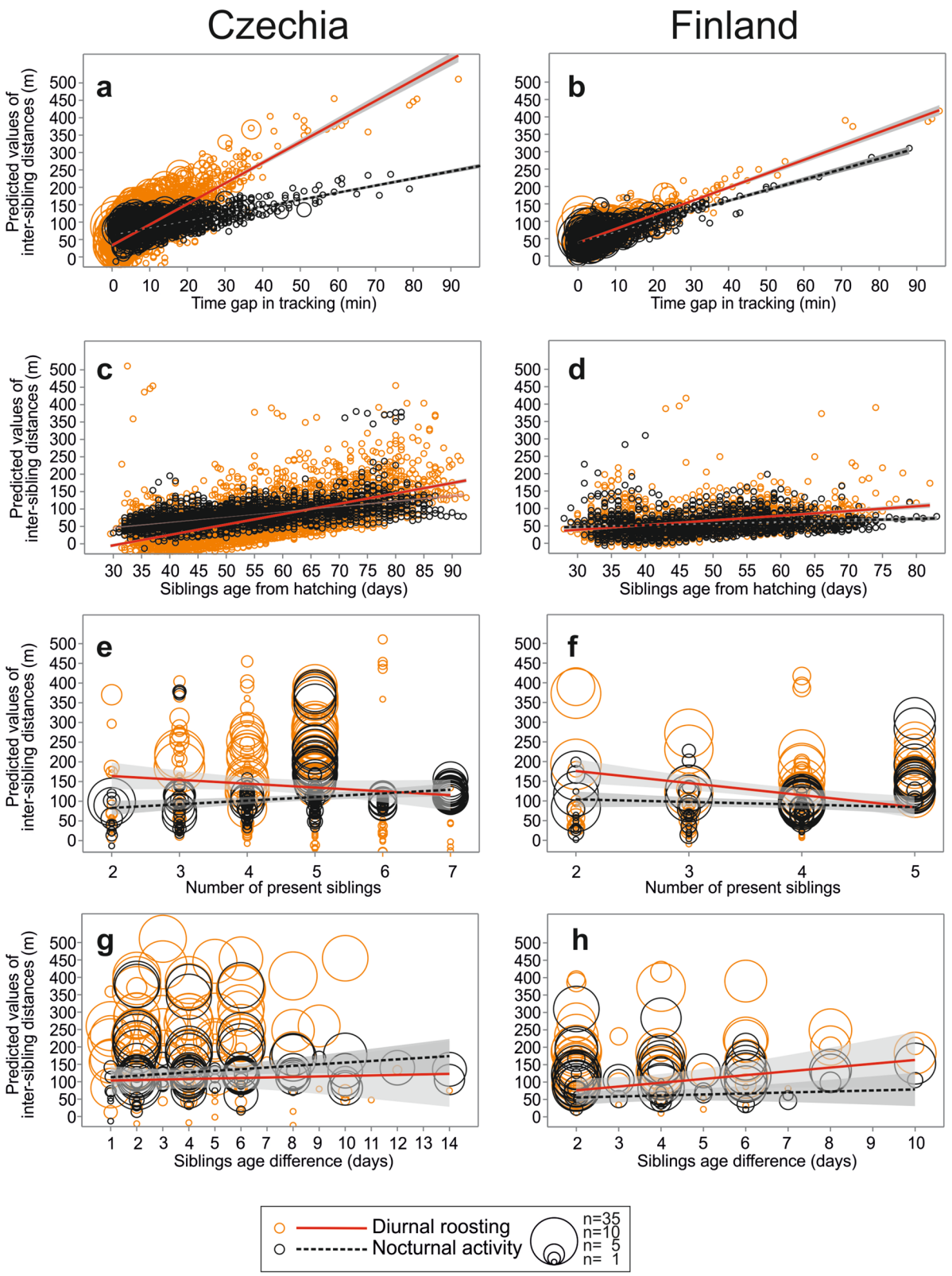

Fig. 1 (See legend on previous page.)

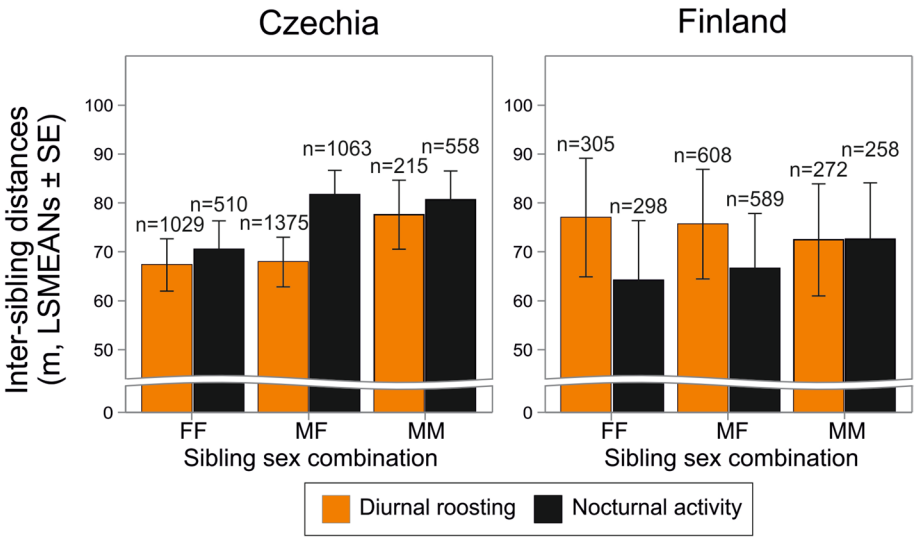

Fig. 2 Sex-related inter-sibling distances. Least square means of inter-sibling distances (LSMEANs ± standard error [SE]) of boreal owl fledglings recorded throughout the post-fledging dependence period within the nocturnal activity (Night) and diurnal roosting (Day) in the study area of Czechia and Finland. Data for sister-sister (FF), brother-sister (MF) and brother-brother (MM) distances are depicted

across distinct areas and behaviourally reversed night and day phases suggests the involvement of the same biological factors, although their effects were modified by local environments in both areas, as the distances differed across the two study sites and periods. Though the results suggest that multiple divergent interests for siblings/fledglings are at play across study sites and periods during the PFDP, the findings of our study support two cooperation hypotheses, antipredation (H3) and negotiation (H4), to be involved in determining the inter-sibling distances during the PFDP rather than the competition (H1) or cooperation-friendship (H2) hypotheses (see bold-noted sub-hypotheses in Table 5).

We did not find support for the competition hypothesis (H1) because inter-sibling distances during the PFDP were not shorter at night compared to day in Czechia (see (a) in Table 5), and were also overall unaffected by the age differences between siblings (b) and the sex of siblings (c). If the distances were determined by competition, we had to identify the latter two factors as influential, because there indeed is a dominance hierarchy among siblings due to asynchronous hatching [44], and female

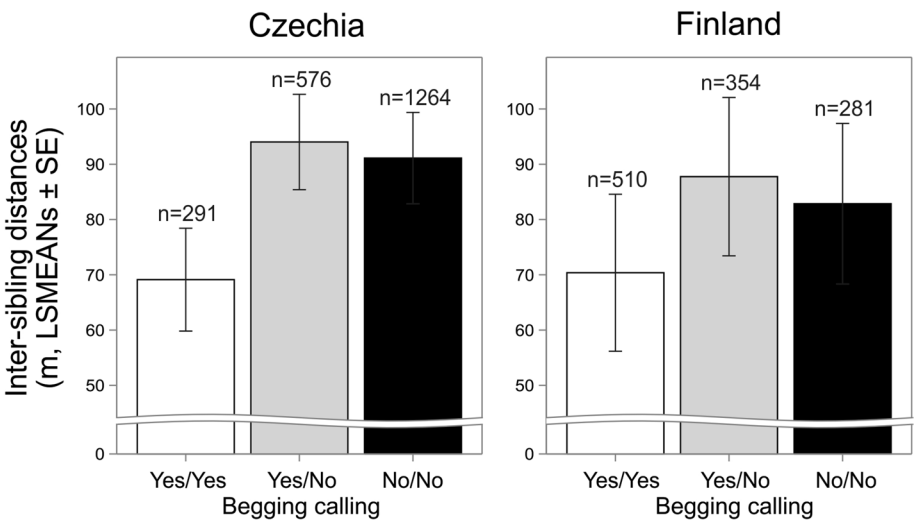

Fig. 3 Begging calling-related inter-sibling distances. Least square means of inter-sibling distances (LSMEANs ± standard error [SE]) of boreal owl fledglings recorded during nocturnal activity throughout the post-fledging dependence period in the study area of Czechia and Finland. Data for sibling pair distances in which both were heard begging for food (YY), only one of them was heard begging (YN) and both were silent during the night (NN) are depicted

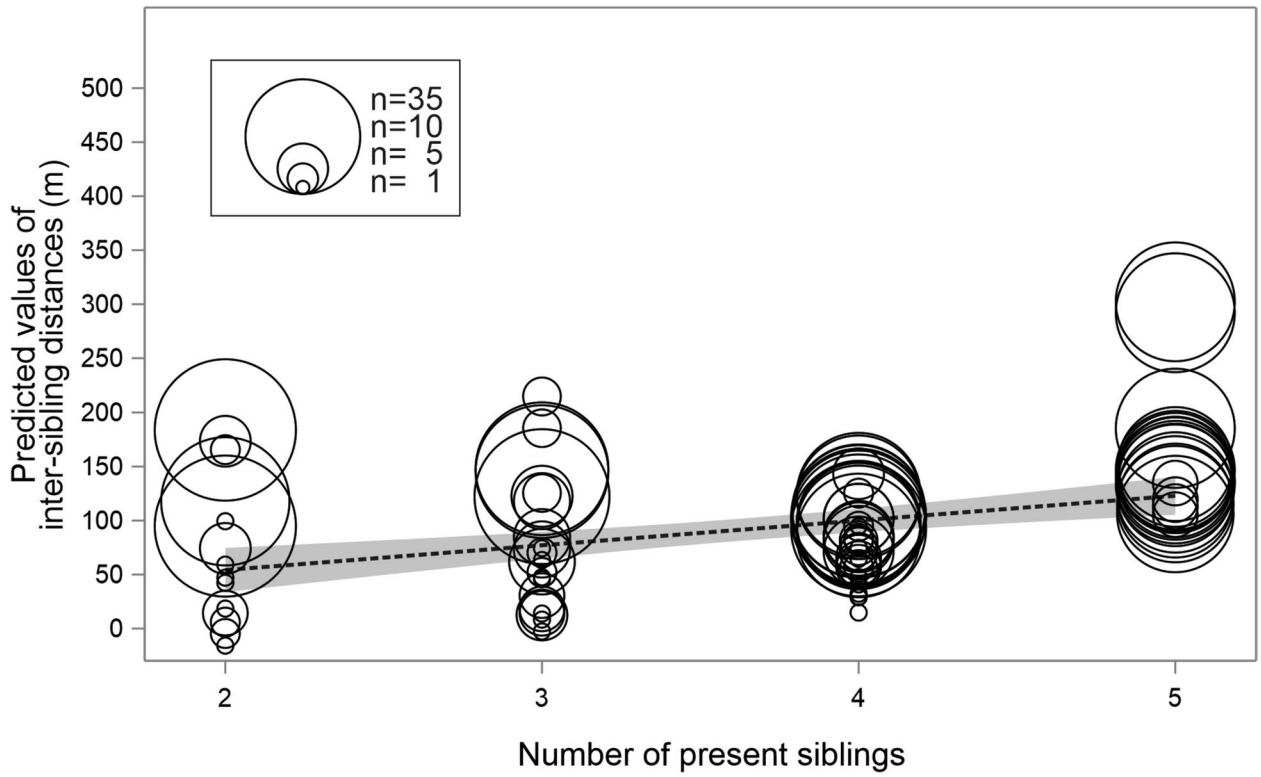

Fig. 4 Present siblings-related inter-individual distances in Finland. Predicted values of inter-sibling distances of boreal owl fledglings recorded throughout the post-fledging dependence period in the Finnish study area during the nocturnal activity plotted against the number of present siblings with a regression line and 95% confidence intervals. The bubble size corresponds to the number of predicted (overlapping) cases between 1 and 35

Table 5 Main alternative hypotheses presuming the biological role of inter-sibling distances. The four main hypotheses (H1–H4) postulated to address whether the inter-sibling distances of boreal owl fledglings recorded throughout the post-fledging dependence period in the study area of Czechia and Finland during the nocturnal activity (Night) and diurnal roosting (Day) are determined either by siblings' competition or cooperation (friendship, antipredation and/or negotiation behaviour). Six effects of different explanatory variables are stated that can either confirm (yes) or reject (no) the validity of each of the main hypotheses. The rationale for the specific sub-hypotheses (a–k) is provided in the main text at the begining of the Methods section. The sign (yes/no) for the sub-hypotheses, which were verified within the statistical analysis, is shown in bold text (sub-hypothesis "g" was verified for the Day only)

Hypothesis	No	Distance shorter during Night compared to Day	With increasing siblings' age – distance decreases	With increasing siblings' age difference – distance decreases	With increasing number of siblings – distance decreases	Distances between M-M and/or F-F sibling pairs shorter than in M-F pairs	Distances shorter in begging calling siblings compared to silent ones
Competition	H1	Yes[(a)]	-	Yes[(b)]	-	Yes[(c)]	-
Cooperation – Friendship	H2	No[(d)]	Yes[(e)]	-	-	-	-
Cooperation – Antipredation	H3	**Yes/no**[(f)]	-	-	**Yes**[(g)]	-	-
Cooperation – Negotiation	H4	**Yes/no**[(h)]	-	-	-	-	**Yes**[(k)]

siblings can be expected to be competitively superior due to their larger body size [33, 45]. It is also possible that the situation after fledging changes so fundamentally that the hierarchy ceases to exist, and/or that the smaller brothers might have better manoeuvrability [46, 47] and can escape their sisters at any time. However, it is essential to note that over several years and thousands of localisations and direct sightings of fledged siblings, we never

recorded a single case of siblings robbing each other of a prey item delivered by their parent. This is further supported by our previous findings on begging call behaviour patterns in boreal owl fledglings during the PFDP [11], which support the theory that begging calling is an honest signal of the need to parents [5, 48] rather than a signal of conflict/competition [49].

Our results disagreed with the cooperation-friendship hypothesis (H2) because, at both study sites, inter-sibling distances differed between the night and day phases (d) and increased with siblings' age throughout the PFDP (e), thus being inconsistent with both predictions. Based on the results, it is clear that biological factors, such as improved antipredation and/or communication tactics, help maintain specific inter-sibling distances during the PFDP. However, the siblings do not hold together due to the sense of inter-individual affection established during the nestling period.

Consistent with the predictions of the cooperation-antipredation hypothesis (H3), the mean inter-sibling distances were shorter in Finland compared to Czechia during both day and night (f), and inter-sibling distances were shorter at both sites within larger sibling flocks during the day (g), but longer at night, which was unexpected. Nevertheless, everything indicates that this finding does not necessarily undermine the antipredation hypothesis (H3). In fact, these results, and particularly the fact that the models with fixed effects nested within the daytime period (day/night) performed better than the non-nested models, clearly show that we must strictly separate siblings' behaviours during nocturnal activity and diurnal roosting. The two phases differ markedly in environmental aspects, such as optical conditions and the composition of predators and their hunting strategies, as well as in behavioural aspects, including fundamentally different interests and priorities of siblings/fledglings during nocturnal or diurnal activities. This is further emphasised by the opposite effect of the number of present siblings on nocturnal inter-individual distances in Finland when night and day data were analysed together or separately (Figs. 1f and 4). During the night, the centre of the fledglings' attention is the prey items brought by the parent, as they are hungry after a long daytime roosting period, and acting in an anti-predation manner is probably secondary compared to the day. In both study areas, during the day, the more critical period regarding antipredation, because the fledglings are not active, the siblings stayed closer to each other with their increasing number, suggesting involvement of the "group vigilance" and "individual risk" hypotheses [50, 51], thus reducing predation probability and supporting the antipredation hypothesis.

The most important finding, which supports the cooperation-negotiation hypothesis (H4), is that begging-calling siblings were closer to each other than those that were not begging for food (k). This suggests that siblings attempt to beg for food in a certain proximity to each other, allowing them to "agree" on who will receive the next prey brought by their parent. Therefore, we interpret that during nocturnal activity within the PFDP, boreal owl siblings negotiate access to the following prey item, similar to barn owl (*Tyto alba*) nestlings during the nestling phase, as thoroughly shown by [9, 15, 16]. If not caused by the negotiation efforts, there would be no reason for calling/begging siblings to stay closer to each other, and a better strategy would be, for instance, to anticipate the direction from which a parent appears and move and beg in that direction, as is the case with silent individuals. These individuals were most likely already satiated and interested in other matters, such as exploring the surroundings or possibly acting in line with antipredation strategies.

The distances during the night were definitely short enough in both study areas to allow siblings for effective negotiation (even humans can hear the boreal owl fledglings' begging calls up to a few hundred meters during good weather), and were shorter in Finland than in Czechia (h), as sibling negotiation is probably more crucial in Finland. It is because the hunting period in Finland, over which the fledglings can be fed, is at least two times shorter compared to Czechia [33, 52], and cases of fledgling starvation to death were recorded in the Finnish study area even during the year with relatively high prey abundance, which was not observed in the Czech study site [43, 53]. Similarly, the fledglings in Finland were vocally begging for food, usually throughout the night, even during the rich food season (M. Kouba and E. Korpimäki, unpublished data). In contrast, in such seasons, the Czech individuals were often silent [11]. Therefore, we suggest that due to the more challenging environment, siblings in Finland are forced to stay closer to each other and focus primarily on effective cooperation/negotiation through begging calls during the night. Moreover, the boreal owl fledglings vocalise (beg for food) intensely and loudly throughout the night if hungry [11], making them easy targets for any nocturnal predators, such as Ural owls (*Strix uralensis*) [54]. Thus, focusing primarily on antipredation during nocturnal activity makes no sense unless they are satiated.

The tracking time was found to be non-influential already during the exploratory phase of the analysis. This result further supports the antipredation hypothesis (H3), as siblings should attempt to avoid predation regardless of the time of day. In addition, this result is also inconsistent with the prediction of the competition hypothesis

(H1), which states that siblings found at an early night should be closer to each other than those found at a late night. The reason is that at the start of the night, they are indeed hungry after long daylight hours, regardless of prey abundance. Therefore, a possible opportunity to rob others of a prey item is probably high at early night, while decreasing at late night, because the parent begins to feed and gradually satiates the offspring. In line with this would be the finding that boreal owl fledglings beg for food less as the night progresses [11].

We found that the boreal owl siblings spend their time during the PFDP alone, i.e. in the absence of their parent (particularly during their diurnal roosting; M. Kouba and E. Korpimäki, unpublished data), but not without parental care. The presence/absence of parents and/or parental care has been shown to substantially influence social interactions among siblings. In burying beetles (*Nicrophorus vespilloides*), when parents provide parental care, siblings evolve to compete, and *vice versa*; they cooperate in their absence [55]. Similarly, juveniles of the cichlid fish (*Pelvicachromis pulcher*) compensated for the absence of parental care by exhibiting improved shoaling behaviour, thereby reducing predation risk [56]. It was suggested that bird foraging flocks benefit from group living through increased foraging efficiency, enhanced predator detection probability, dilution of individual risk and confusion of predators during attacks [51, 57]. Though the scenario in boreal owl sibling groups is undoubtedly different, we might speculate that the absence of boreal owl parents could promote the evolution of inter-sibling cooperation in antipredation and begging-negotiation behaviours. We acknowledge, however, that both these suggestions need to be further explored.

We are aware of some potential shortcomings of our study. For instance, it would be best to localise all the siblings from a single brood at the same time, but even in a much larger team, it would be extremely challenging. There is also a bias in every GPS location collected by a handheld GPS device, due to its precision and the quality of the signals received from satellites. Most locations of fledglings collected in our study were recorded with a precision of ± 3 m, as indicated by the GPS devices used. We surmise that this slight inaccuracy could not bias our analyses and the conclusions drawn from them, because even if the worst possible bias were incorporated into each collected position, the biological conclusions would not change. Finally, though we found no effect of rough habitat composition around the nest boxes (area sizes of clear-cuts, young, mature and old-growth forests) on inter-sibling distances, it is still possible that the detailed interior forest composition and structure could be influential, which we were unable to determine. Effects and their mutual interactions, such as the age of particular trees and their branching, tree species composition, specific forest part densities, etc., could indeed play a role in sibling spacing within their habitat; however, these details of their environment are currently impossible to obtain.

Conclusions

We conclude that the main findings of our study suggest that the inter-sibling distances in boreal owls during the PFDP are maintained because siblings cooperate in terms of collective antipredation behaviour during diurnal roosting and collective negotiation over access to the indivisible prey items delivered by their parent during nocturnal activity. Therefore, the cooperation-antipredation hypothesis is supported during the day, and the cooperation-negotiation hypothesis is supported at night, thus complementing each other. We suggest that cooperation can generally correspond to a specific time of day, depending on the nocturnality or diurnality of the target species and the specific needs of the specimens, based on their life history, such as whether they are predator or prey species. The boreal owl was an ideal study subject in this regard, as it fulfils both roles, enabling us to provide important findings across different daytime periods and the needs of the individuals being studied. Earlier elegant studies showed that barn owl chicks negotiate for access to prey items delivered by their parents at night [9, 15, 16], but this co-operation between siblings happened in the safe nest cavity. Our results, to our knowledge, showed for the first time that cooperation among siblings of the brood likely occurs after fledging (during PFDP) outside the safe nest cavity, where offspring are vulnerable to predators during their daytime roosting and when begging for food at night. It is not possible to compare our results with those of any other similar study because detailed studies on the behaviour of young individuals during the PFDP are lacking in most avian species, particularly in birds of prey and even more so in nocturnal species. If such studies exist, they have focused on parent–offspring interactions (e.g., [18, 58, 59]), rather than sibling relationships. Therefore, we encourage researchers to conduct studies on sibling relationships and behaviours across species during the post-fledging phase (a critical life stage), as this topic has been considerably understudied to date. Such studies could provide new insights into the parent–offspring conflict theory, particularly regarding sibling rivalry and/or cooperation, which have been among the most extensively studied topics in evolutionary biology over the last several decades (e.g., [1, 60, 61]).

Methods

Study hypotheses and their reasoning

The overview of the four main hypotheses (H1–H4) and their corresponding sub-hypotheses (a–k) is provided above in Table 5. The detailed reasoning for the main hypotheses, based on specific sub-hypotheses (competition hyp. H1, sub-hyp. a, b, c; cooperation-friendship hyp. H2, sub-hyp. d, e; cooperation-antipredation hyp. H3, sub-hyp. f, g; and cooperation-negotiation hyp. H4, sub-hyp. h, k) and allowing for confirmation or rejection of the main hypotheses, is as follows.

(a) Inter-sibling distances during the Night should be shorter than during the Day in both countries because the parents deliver prey during the night only [33, 37, 38]. The siblings should be close to each other to have a chance to rob others of a prey item.

(b) Night distances will decrease with increasing siblings' age difference (older siblings will be better able to rob the younger ones of the received prey and should try to be close to them).

(c) Night brother-sister distances will be shorter compared to the distances between brothers or sisters because females are approximately 5% heavier, thus competitively stronger [33, 62], and possibly able to rob their brothers.

(d) The distances should be relatively stable throughout the PFDP during both the Night and Day because individual siblings will continuously keep their inter-sibling distance.

(e) The distances will decrease during both Night and Day with the advancing age of the siblings, because they gradually increase their flying ability [41]; thus, being closer to each other should be easier.

(f) The distances will be shorter during both the Night and Day in Finland, where the overall predation pressure (mainly by birds of prey) is much higher than in Czechia [43, 53]. Being closer to each other should be advantageous regarding both the "group vigilance" and "individual risk" hypotheses [50, 51], thus reducing predation probability. In contrast, inter-sibling distances regarding predation risk are not crucial in Czechia because local fledglings are primarily predated by pine martens (*Martes martes*), and this occurs only a few days after fledging [43].

(g) According to the "group vigilance" and "individual risk" hypotheses, the inter-sibling distances would also decrease with the number of present siblings during both study periods and within both study sites.

(h) The distances during the Night would be short (tens of meters at most) to allow siblings to negotiate effectively about who will receive the next indivisible prey item and should be shorter during the Night in Finland than in Czechia. This is because the prey is delivered by parents only at night [33, 37, 38], which is much shorter in Finland. Consequently, sibling negotiation is likely to be more crucial in Finland and more effective when siblings are closer.

(k) The distances would be shorter between siblings that were heard producing begging calls than between those that did not beg for food, because if they indeed negotiate access to food delivered by parents, it is more effective when they are relatively closer to each other.

Study areas

The study was conducted over six breeding seasons in Czechia from 2010 to 2012 and 2015, and in Finland in 2019 and 2021. The Czech site (50° N, 13° E) is situated in the Ore Mountains and included 120–170 nest boxes (see details in [35, 36]). The study area was severely damaged by historical air pollution events (for more information, see, e.g., [36]). Currently, the area is mainly forested, predominantly by blue spruce (*Picea pungens*; covering approximately 28% of the area), Norway spruce (*Picea abies*; 26%), birch (*Betula* spp., 11%), European mountain ash (*Sorbus aucuparia*, 5%), European beech (*Fagus sylvatica*, 4%) and European larch (*Larix decidua*, 4%) [36].

The Finnish site is located in the Kauhava region of western Finland (63° N, 23° E) and comprised 450 nest boxes (see details in [30, 63]). Approximately 61% of this study area is forested, with the predominant species being Scots pine (*Pinus sylvestris*, forming ca. 65% of the local forests), Norway spruce (> 30%), and a minority of deciduous trees (birches and Eurasian aspen, *Populus tremula*) [30].

The length of the night during summer in Czechia is approximately twice as long as in Finland. The sites also differ in altitude and weather; the Czech site is in a mountainous region, resulting in higher altitudes, colder temperatures and more precipitation compared to the Finnish site (see details in Additional file 1: Table S1). The habitat conditions also vary, particularly in terms of forest stand age, structure and composition. The forests on the Czech site are composed of small stands of relatively old and dense Norway spruce, as well as extensive areas of loose stands of non-native, young blue spruce. In comparison, the forests of the Finnish site are heavily managed, with dense middle- and old-age forest patches scattered between open clear-cut areas and dense young forests (see [36, 53], for further details). Further, prey abundances vary between the two study areas within particular years [42]. Predator communities are also very

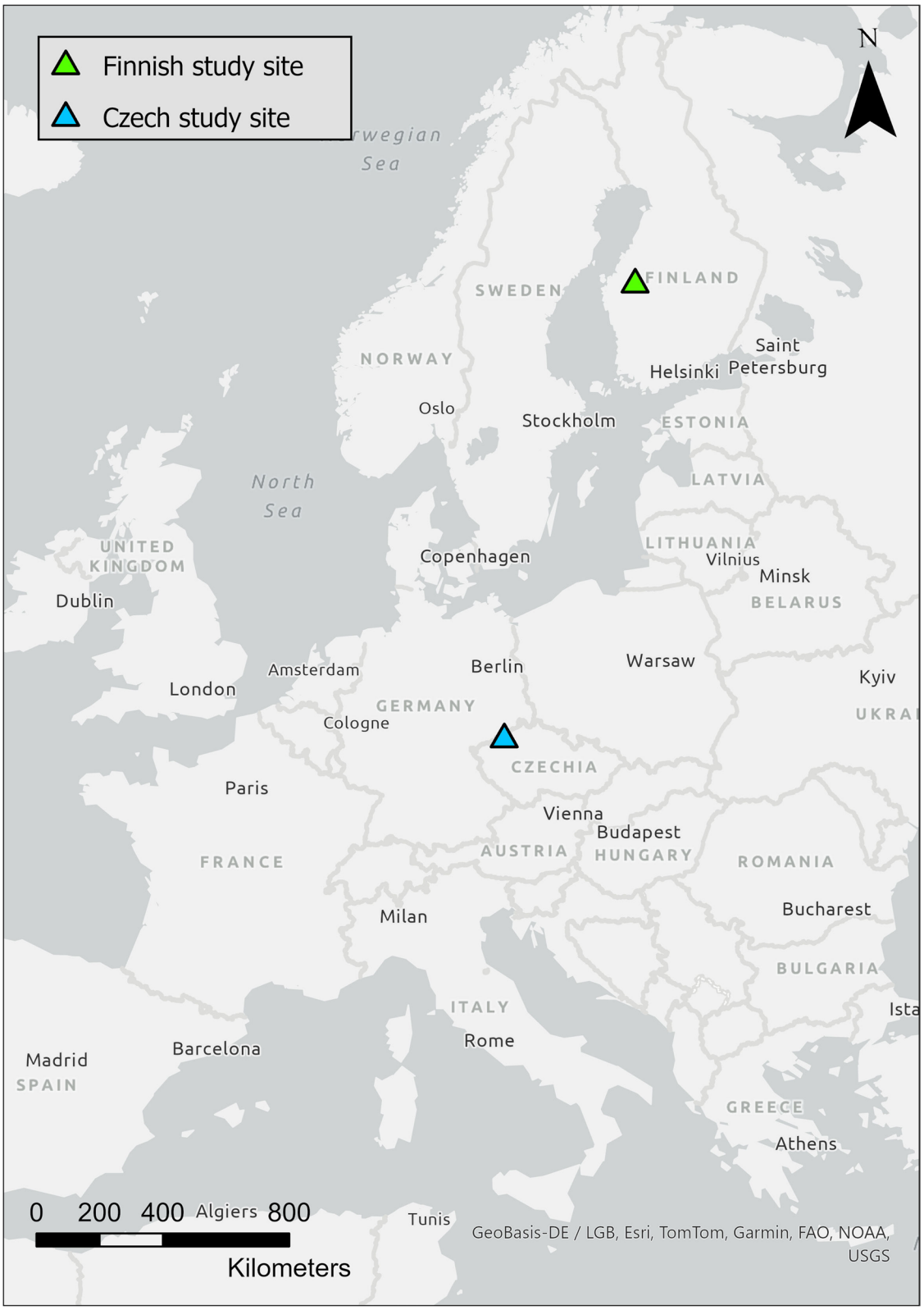

Fig. 5 Location of both study areas. The Finnish study area (Kauhava region; green triangle), situated in Northern Europe, and the Czech study area (Ore Mountains; blue triangle), located in Central Europe, are depicted (ArcGIS Pro version 3.2.0, https://www.esri.com; the map was created based on a licence granted to the Czech University of Life Sciences Prague)

different, composed mainly of birds of prey [primarily northern goshawks (*Accipiter gentilis*) and Ural owls] in Finland but of pine martens in Czechia [43]. The two study sites are approximately 1500 km apart (Fig. 5).

The nest boxes in both study areas were similar in design, made of wood, square in section, with a base measuring 18–25 cm × 18–25 cm, a height of 40–60 cm, and an entrance hole diameter of 8–10 cm.

In both study areas, the abundance of potential prey (small terrestrial mammals) was assessed using snap traps set in late spring (early June at the Czech and early May in the Finnish site). Snap-traps were set up in squares spaced 10 m apart and checked each morning for three consecutive days. For each year of the study, the total trapping effort was 1089 trap nights ($n = 3$ locations) at the Czech study site, and approximately 600 trap nights ($n = 8$ locations) at the Finnish study site. The number of captured mammals per 100 trap nights was calculated for each study site and breeding season (Table 1).

Field and laboratory procedures

We regularly visited all nest boxes in both study areas and across all study years from early March to late June to find nests. If nesting was identified, nests were checked frequently enough to determine the number of eggs and hatchlings, as well as the exact hatching date (± 1 day). The age of the nestlings was determined from the recorded hatching dates. Fifty microliters of blood was collected from each nestling by brachial vein puncture under the wing approximately 14 days after hatching for molecular sexing [64]. The later laboratory sex determination of blood sampled nestlings was performed according to the method developed by [65].

From 25 days after the hatching of the first chick, we checked the nest boxes at 1- or 2-day intervals. All individuals were weighed, and the wing length was measured to estimate the appropriate time for tagging [11, 36]. Nestlings were equipped with a type PIP4 leg-mount radio-transmitter (Biotrack Ltd., UK) 27 ± 2 (mean ± SD) days after hatching and 5 ± 2 days before fledging. Together with the tail-mount, the leg-mount attachment method was suggested as the best possible, as it appears to have the least adverse effects [66]. Following the procedures of [36], nest boxes were visited at 12-h intervals during the night (22:00–04:00 in Czechia; 23:00–03:00 in Finland) and during daylight (10:00–21:00 in the Czech Republic; 8:00–21:00 in Finland) until all siblings had fledged and the exact date of nest box departure was determined. The transmitter weight within all six seasons was 2.5 ± 0.5 g (± SD) on average (lifespan ± 10 weeks), following welfare recommendations that the transmitters should not exceed 3% of the body mass of the tagged individuals (e.g., [67]).

After fledging, the young were radio-tracked using the "homing-in" method [68], in which the signal is followed to a particular tree or until the individual is observed, becomes independent, is found dead or disappears. Fledglings were located approximately every 24 h, i.e., once every night in 2010 and 2011, and once every day in 2015 (Czechia). In 2012 (Czechia), 2019 and 2021 (Finland), they were located approximately 12 h apart, i.e., once every night and once every day. Radio signals were monitored using Yupiteru MVT-9000 receivers (Yupiteru Industries Co. Ltd., Japan) and 3-element Yagi antennas. Fledglings' positions were recorded using handheld GPS receivers (Garmin GPSmap 60CSx or Astro 230, Garmin Ltd., USA). Different behaviours of fledglings were recorded during and after their location, including presence/absence data on begging calling [11]. The PFDP begins with the owlets' departure from the nest and ends with the first rapid, abrupt movement away from the fledglings' habitual locations, an event that previous studies have suggested may correspond to the cessation of begging for food [11, 36].

Statistical analyses

We used SAS System version 9.4 (SAS Institute Inc.) to analyse the data in four steps. First, analyses were conducted to check for intercorrelation and multicollinearity in the data from the boreal owl study population, weather, and habitat composition, separately. We subsequently assessed the extent of collinearity by examining related statistics, such as Tolerance values, Variance Inflation Factors, Eigenvalues and Condition Numbers, following the approach of [69] and using the TOL, VIF and COLLIN options of the MODEL statement in the SAS REG procedure. Correlations are generally considered "strong" above 0.8 [69] or at least 0.5 [70]. In further analyses, no variables found to be intercorrelated or collinear were used together in the same model.

Second, we calculated all the inter-sibling distances based on the recorded GPS locations of their occurrence within particular day phases (daytime and nighttime), after projecting all locations to a local metric coordination system: S-JTSK/Křovák East North (EPSG: 5514) for the dataset from Czechia, and ETRS-TM35FIN (EPSG: 3067) for the dataset from Finland. We measured the straight distance between all pairs of siblings within broods with two or more siblings, thereby obtaining the dependent variable, the "inter-sibling distance". There was typically at least a 1-day gap between daytime and nighttime measurements, during which the siblings were usually relocated. This meant we could consider the individual distance measurements between the siblings as independent. Consequently, we were able to analyse how these distances change over time in relation

to daily variations in other fixed effects. Subsequently, we calculated all other variables for given pairs of siblings connected with the specific distance measured. Thus, we obtained data for the variables/fixed effects, which we tested in the analyses below (after excluding all intercorrelated variables within the first step). Within the subsequent exploratory analysis, we followed the procedures outlined by [41, 53] to reduce the number of models tested, thereby preventing overfitting in the final models. Specifically, we tested and omitted the following non-influential variables: individual sibling characteristics, such as wing length and scaled mass index; environmental characteristics, including cover of open lands, clear-cut areas and young, mature, and old-growth forests within a circle of 500-m radius around the nesting box; and the time of tracking. The fixed effects used in the final analyses were as follows: hatching date, siblings' age from hatching, siblings' age difference, sex of siblings, number of present siblings, time gap in tracking, daily precipitation, presence/absence of begging calling and spring prey abundance (see explanations of the variables used and their units in Table 2). To validate the data inspection finding that conditions differ between the two countries, the Kruskal–Wallis test (Proc Univariate) was applied to assess differences in inter-sibling distances in Czechia and Finland.

Third, we applied model selection based on the information-theoretic paradigm using Akaike's Information Criterion (IT-AIC) [40]. After testing for multicollinearity and conducting exploratory analysis (see above), we formulated a priori multiple hypotheses based on the remaining biologically relevant variables (each model/hypothesis tested, including the biological explanations of the fixed effects applied, is listed in Additional file 1: Tables S2 and S3). The combination of fixed effects in the alternative models tested was dependent on the formulation of a priori hypotheses.

Since the introduction of Akaike's Information Criterion (AIC; [71]), various information criteria have been developed, each with distinct mathematical properties and philosophies of model selection in mind [72]. Following [72], we used expanded information criteria AIC, BIC, CAIC and HQIC to select the true model. We calculated Δ_i (the differences between the Fit statistic values, the smallest values indicating the best-fitting model), w_i (the weight, interpreted as the probability that M_i is the best model) and w_{min}/w_j (for estimating the strength of evidence in favour of one model over the other—AIC or BIC, CAIC, and HQIC Odds) [73] for all four fit criteria AIC, BIC, CAIC and HQIC [72]. Since there was a similar or identical rank order across these criteria and Δ_i, w_i and w_{min}/w_j yielded similar results, we present the AIC values (e.g., [74, 75]) only as an illustration (Table 3 and Additional file 1: Table S4).

To find out whether the best model has merit, we compared our best model to the null model for the dependent variable using Δ AIC (for AIC, AIC null – AIC best model; the same was also calculated for BIC, CAIC, and HQIC; Table 3 and Additional file 1: Table S4) and a relative information loss [for AIC exp((AIC_null – AICi_best)/2); the same for BIC, CAIC, and HQIC], an approach adapted from [73].

Fourth, two different models (I, II; Table 3) were analysed using the General Linear Mixed Model (GLMM; PROC MIXED), with fledged siblings' distances during the PFDP in Czechia or Finland (predictions H1–H4) as the dependent variable. The fixed effects were nested within the daytime period "day/night" in one-third of the competing models (Additional file 1: Table S2). Two additional models (III and IV; see Table 3) were analysed using the same procedure and dependent variable, but specifically during nocturnal activity, as boreal owl fledglings only beg for food at night [11]. To evaluate the effect of siblings' begging calls on the distance between siblings, we established a slightly modified set of a priori hypotheses/models (see Additional file 1: Table S3). All four models (I–IV) included the variable nest box ID as a random intercept for the grouping variable to account for non-independence of observations within each brood. For the graphs, we estimated associations between the dependent variable and the fixed effects by fitting a random-coefficient model using PROC MIXED, as described by [76].

Abbreviations

PFDP	Post-fledging dependence period
SD	Standard deviation
AIC	Akaike Information Criterion
GPS	Global positioning system
EPSG	European Petroleum Survey Group
IT-AIC	Information-theoretic paradigm using Akaike's Information Criterion
BIC	Bayesian Information Criterion
CAIC	Consistent Akaike Information Criterion
HQIC	Hannan-Quinn Information Criterion
GLMM	General Linear Mixed Model

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12915-026-02626-3.

Additional file 1: Supporting information tables. Description of data: Tables with additional information not included within the main manuscript body due to space reasons.

Additional file 2: Raw data. Description of data: Raw data used during statistical analysis on which the study results and conclusions are based.

Acknowledgements
We thank Alena Popelková for her assistance with nest box controls and tagging the nestlings from 2010 to 2012, Alessandro Fantoni for his help with tagging the nestlings and radio-tracking in 2015, and Jiří Šindelář for his assistance with nest box controls in 2015 in the Czech Republic. We also thank Tomáš Bušina, Jorma Nurmi, Kari Hongisto, and Martin Janouš for their help in the field throughout the study in Finland. We greatly appreciate Lubomír Peške for his technical assistance with radiotelemetry and manufacturing Yagi antennas for the whole study. Next, we would like to thank two anonymous reviewers for their comments and suggestions on the earlier draft of the manuscript. The article processing charge was covered by the Faculty of Agrobiology, Food and Natural Resources at the Czech University of Life Sciences Prague.

Authors' contributions
LB and MK are the principal contributors and conceivers of this study. MK, SSS, FT, and EK collected the field data. MŠ, MK, and FT prepared and processed the spatial data. SSS performed laboratory sexing on the Finnish nestlings. MK and LB wrote the draft manuscript, and EK edited it. LB and MK prepared the figures. JB prepared scripts for statistical analysis. LB and MK did the statistical analysis. All authors read and approved the final manuscript.

Funding
The research project was financially supported by three grants from the Regional Fund of South Ostrobothnia of the Finnish Cultural Foundation (Grant Nos. 0116947–3, 10201775, and 10241809).

Data availability
All data generated and/or analysed during this study are included in this published article (and its supplementary information file, the Additional file 2).

Declarations

Ethics approval and consent to participate
Owls in Czechia were trapped, handled, blood sampled and tagged under Permits Nos. 530/758 R/08-Abt/UL, 35016/02-OOP/8751/02, and 173/049/ZPZ/2015/ZD-838 issued by the Ministry of the Environment of the Czech Republic. The birds were ringed under the supervision of the Ringing Centre of the National Museum in Prague, Permit No. 329. Fledglings in Finland were tagged and radio-tracked under the approval of the Centre for Economic Development, Transport and the Environment (Varsinais-Suomen Elinkeino-, Liikenne- ja Ympäristökeskus: Permit No. VARELY/1389/2018), ringed under the ringing licence of the Finnish Museum of Natural History (Licence No. 524). Blood samples were taken under the approval of the Animal Experiment Committee of the State Provincial Office (Etelä-Suomen aluehallintovirasto ESAVI; Permit No. ESAVI/3021/04.10.07/2017). All efforts were made to minimise suffering.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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Received: 28 January 2026 Accepted: 7 May 2026
Published: 18 May 2026

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