1   **EXPERIMENTALLY DISENTANGLING INTRINSIC AND EXTRINSIC DRIVERS OF NATAL**

2   **DISPERSAL IN A NOCTURNAL RAPTOR**

3   Julien Fattebert[1,2*], Marco Perrig[1], Beat Naef-Daenzer[1], Martin U. Grüebler[1]

4   [1]Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

5   [2]Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal,

6   Durban 4000, South Africa

7   *Corresponding author: julien.fattebert@gmail.com

8   Running head: Drivers of dispersal in little owls

9

10 **ABSTRACT**

11 Equivocal knowledge of the phase-specific drivers of natal dispersal remains a major deficit in

12 understanding causes and consequences of dispersal and thus, spatial dynamics within and

13 between populations. We performed a field experiment combining partial cross-fostering of

14 nestlings and nestling food supplementation in little owls (*Athene noctua*). This approach

15 disentangled the effect of nestling origin from the effect of the rearing environment on

16 dispersal behaviour, while simultaneously investigating the effect of food availability in the

17 rearing environment. We radio-tracked fledglings to quantify the timing of pre-emigration

18 forays and emigration, foray and transfer duration, and the dispersal distances. Dispersal

19 characteristics of the pre-emigration phase were affected by the rearing environment rather

20 than by the origin of nestlings. In food-poor habitats, supplemented individuals emigrated

21 later than unsupplemented individuals. In contrast, transfer duration and distance were

22 influenced by the birds' origin rather than by their rearing environment. We found no

23 correlation between timing of emigration and transfer duration or distance. We conclude that

24 food supply to the nestlings and other characteristics of the rearing environment modulate

25 the timing of emigration, while innate traits associated with the nestling origin affect the

26 transfer phases after emigration. The dispersal behaviours of juveniles prior and after

27 emigration therefore were related to different determinants, and are suggested to form

28 different life-history traits.

29 **KEY-WORDS**

30 *Athene noctua*, cross-fostering, food supplementation, little owl, natal dispersal, radio-

31 tracking

1. Introduction

Natal dispersal is a fundamental life-history stage in many species [1–3], and is considered to be under strong selective pressure [4–6]. Although natal dispersal is pivotal in linking animal population dynamics to large spatial scales by redistributing individuals [7,8], limited and equivocal knowledge of the drivers of the spatiotemporal patterns of dispersal at the individual level remains a major deficit in understanding the causes and functions of natal dispersal at the population level.

Life-history theory posits that natal dispersal is ultimately driven by avoidance of inbreeding, avoidance of competition for resources or mates, or combinations thereof [9–11]. Thus, selection can shape dispersal traits that allow flexible adjustments of the dispersal behaviour in relation to changing environmental contexts [5,12]. Proximate drivers of dispersal are plastic, multi-causal, and context-dependent [13–16], and thus, cause complex dispersal patterns [17]. Plasticity of dispersal can occur in each of the three distinct phases of dispersal: emigration, transfer, or settlement [18]. On the one hand, proximate factors can be related to intrinsic prenatal factors, such as maternal effects [12], genetics [19,20], or epigenetics [21]. On the other hand, the environment in which offspring develop, such as habitat characteristics [22], parental performance or population density [23–25], can have important extrinsic effects on an individual's dispersal decisions [15]. Phenotypic traits [26] or early dispersal decisions associated with intrinsic or extrinsic factors can correlate with decisions in later dispersal phases, and thus can form a behavioural syndrome predictive of the outcome of dispersal [15,27].

Among environmental factors in the rearing environment, food resources are thought to play a major role in modulating dispersal rates and distance through intraspecific competition

55   [13,28]. Food availability also affects pre-dispersal body condition [29–31], potentially

56   resulting in condition-dependent dispersal. Also, food availability may affect a trade-off that

57   individuals face in the timing of emigration: early dispersers may encounter a higher

58   availability of vacant potential breeding sites, while late dispersers may profit from improved

59   energy reserves, experience, or competitive abilities [32,33]. However, the effects of food

60   availability in the rearing environment on dispersal characteristics can be confounded by

61   intrinsic prenatal factors and by correlations with other factors in the rearing environment

62   [28,34,35]. To our knowledge, approaches to disentangle these effects experimentally were

63   very limited so far.

64   Herein, we present a field experiment in little owls (*Athene noctua*) combining partial cross-

65   fostering of nestlings to control for nestling origin, and food supplementation to manipulate

66   nestling food supply in a landscape with a natural gradient of habitat suitability. We radio-

67   tracked the juveniles from fledging to their first settlement. We characterized dispersal phases

68   – exploratory forays, permanent emigration, transfer, and settlement - based on movement

69   modes obtained from the individual trajectories [36]. In the food supplementation

70   experiment, we experimentally disentangled the effect of food availability from other factors

71   related to the rearing environment while controlling for habitat suitability as experimental

72   effects might differ in relation to natural food availability [37]. We tested two alternative

73   hypotheses of the effect of food supplementation on dispersal behaviour simultaneously

74   controlling for natural habitat suitability. Under a 'delayed emigration hypothesis', we predict

75   a later emigration in food-supplemented broods compared to unsupplemented broods

76   [32,33]. In contrast, under an 'advanced emigration hypothesis', we predict an earlier

77   emigration in food-supplemented broods compared to unsupplemented broods [38,39]. At

78   the same time, the partial cross-fostering experiment disentangled the effects of the rearing

4

79   environment including food availability from the potential effect of nestling origin on dispersal

80   characteristics. This also allowed investigating the relative importance of the effects of origin

81   and rearing environment in the course of natal dispersal. These experimental insights clarify

82   the determination of timing and duration of different phases of natal dispersal, and show how

83   factors determining early pre-emigration dispersal phases carry-over to later post-emigration

84   dispersal phases.

85   **2. Material and methods**

86   **(a) Study area and study species**

87   The little owl is a territorial, nocturnal, generalist avian predator of about 200 g and lives in

88   various open habitats. We studied natal dispersal in a nest-box population of little owls in the

89   Ludwigsburg District in Baden-Württemberg, southwest Germany (48° 53.6' N; 9° 11.6' E; 250

90   km^2) in 2009-2012 [29–31,37,40,41]. In recent studies in the same population, experimental

91   food supplementation positively affected nestlings' growth, body condition and survival

92   [29,30], and adults' reproductive success was shown to be positively related to habitat quality

93   in terms of food availability [31,37]. Little owls have a monogamous mating system with

94   biparental care and obligate dispersers [42]. Moreover, little owls being non-migratory,

95   dispersal decisions are not confounded by seasonal migration. Ring recovery studies found a

96   female-bias in net dispersal distances [42].

97   **(b) Brood monitoring and tagging**

98   From beginning of April to mid-July, we checked occupied nest boxes weekly until clutches

99   were complete. From the earliest expected hatching date until hatching or brood loss, nests

100   were visited every 3-5 days. We visually estimated hatching dates of nestlings through a

101   spyhole using developmental illustrations (commented photographs of nestling for every

102   second day post-hatching starting with day 1, given in [42]). We ringed chicks at c. 14 days old.

103   We determined nestlings' sex genetically using feather samples [30,43]. At c. 4 weeks old,

104   normally a few days before fledging, we tagged the chicks with a VHF radio-transmitter of our

105   own construction mounted with a backpack figure-8-harness (total c. 7 g; 4.5% average adult

106   body mass) [29–31]. Tag range was c. 40 km, and life expectancy was c. 400 days. We tracked

107   each owl by 'homing-in' [44,45] at least three times weekly at night and at least once weekly

108   during the day: for each location a single person followed the signal until the tagged individual

109   could be exactly located without chasing it away. During the main dispersal period in

110   September and October, we recorded 4-5 relocations per individual per week at night. During

111   each tracking event, we were able to identify whether an individual was alive based on its

112   activity.

113   **(c) Experimental treatment**

114   About two weeks post-hatching, at the day of ringing and two weeks before VHF-tagging, we

115   paired 88 synchronous broods as partner broods (44 pairs of broods). We exchanged half of

116   the chicks in each partner brood keeping brood sizes constant (see a timeline of events in

117   Supplementary Material, Fig. S1). Depending on brood size, we selected one or two nestlings

118   of similar age and body weight at c. 14 days old for the exchange. In 30 of the 44 pairs of

119   broods, we randomly assigned one brood to experimental food supplementation, while no

120   food supplementation was applied in the remaining 14 of the pairs of broods due to time

121   constraints in applying the food supplementation treatment. For monitoring and food

122   supplementation after the exchange, all supplementary fed and control partner broods were

123   visited every second day over 36 days until c. three weeks after fledging. Food

124   supplementation started immediately after the exchange, and a total of 480 g of dead

125   laboratory mice per nestling was deposited inside the nest box of each supplemented brood:

126   20 g per visit and per nestling for the first six visits, 30 g per visit and per nestling thereafter

127   [29,30]. This experimental approach created four groups of individuals: (1) individuals reared

128   in their original parental environment, unsupplemented; (2) individuals reared in their original

129   parental environment, food-supplemented; (3) individuals reared in a foster parental

130   environment, unsupplemented; and (4) individuals reared in a foster parental environment,

131   food-supplemented. After the exchange, brood members always shared the same rearing

132   environment including the food supplementation treatment while differing in their origin.

133   Three additional broods for which no synchronous partner brood was available were food-

134   supplemented and the nestling treated as food supplemented individuals reared in their

135   original environment. Furthermore, 146 untreated broods were monitored and VHF-tagged at

136   fledging, and entered the analyses as unsupplemented individuals reared in their original

137   environment.

138   A standard protocol for partial cross-fostering is the exchange of eggs or hatchlings. However,

139   as little owls tend to desert clutches and newly hatched broods after disturbance, we

140   conducted the exchanges around day 14 after hatching. Since energy requirements of

141   nestlings in the first two weeks after hatching are smaller than later in the nestling period and

142   the total period of presence in the rearing environment after the exchange was much longer

143   than the two weeks, we consider the effect of the delay of the exchange to be small. We

144   therefore assume that the delayed cross-fostering treatment only marginally biased the

145   results, and reliably separates the factors related to the nestlings' origin from the factors

146   related to the nestlings' rearing environment.

(d) Habitat suitability

To test for the effect of habitat quality on natal dispersal characteristics, we used a scale-integrated habitat suitability index [46]. We integrated three order-specific resource selection functions to account for conditional dependencies across scales in a single model. For the purpose of the present analyses, we calculated the average habitat suitability score of each breeding home range. Because not every parental pair was radio-tracked, we defined natal ranges as the area within a 300 m radius around the nest boxes based on average adult home range size estimates in this population [31].

(e) Body condition

The nestlings' origin as well as their rearing environment may affect body condition at fledging potentially resulting in condition-dependent dispersal. To test for potential effects of differential body condition we used the fledglings' body mass. We weighted 152 fledglings at an average age of 29.2 days ± 3.6 (SD). We used the residuals of a linear relationship between body mass and age (β = 0.968; 95% CI 0.339, 1.598]; $p < 0.001$) as the age-corrected variable for body condition in the analyses.

(f) Dispersal timing, duration and distance

We defined exploratory forays as temporary moves of fledglings beyond a 300 m radius from the nest box, which represents the average size of an adult home range, followed by a return into the natal range. We defined the foray period as the time from the first foray to permanent emigration, i.e. when an individual permanently exited the 300 m radius of the natal range. Starting with permanent emigration, we fitted a hidden Markov model (HMM) to the post-

168   emigration dispersal trajectories using the R package 'moveHMM' [47] to identify three

169   distinct movement modes: (i) directional movement (transfer), (ii) encamped movement

170   indicating home-ranging (settlement); and (iii) an intermediate mode of encamped movement

171   within a temporarily visited area (stopover). Specified starting values for the initial parameters

172   for gamma and von Mises distributions are reported in the electronic Supplementary Material

173   (S2). We then used the change points between successive movement modes to define the

174   timing and the duration of the dispersal phases [48]. Herein, we restricted our analysis to the

175   timing and duration of the exploratory and transfer phase until first settlement. We measured

176   the net dispersal distance as the Euclidean distance between the nest box of fledglings, and

177   their first settlement location.

178   **(g) Statistical analyses**

179   Only 160 birds that survived to the first exploratory foray entered the analyses. We analysed

180   the effects of experimental and control variables on five response variables: age at first foray

181   (days), duration of foray (days), age at emigration (days), duration of transfer (days), and net

182   dispersal distance (km) using linear mixed-effects models (LMM). We fitted the LMM's in a

183   Bayesian framework using the R package 'rstanarm' [49]. We square-root-transformed all

184   response variables to meet the assumption of normal distribution of the error residuals. In all

185   models, we included as fixed-effects food supplementation (categorical; supplemented,

186   unsupplemented), average habitat suitability (continuous; score range 0-1), and their

187   interaction as our focal explanatory variables, and we controlled for sex (categorical; female,

188   male) and hatching date (continuous; Julian day). Where food supplementation or its

189   interaction with habitat suitability was an important predictor of the dependent variable, we

190   tested in a second step for a possible indirect effect of food availability mediated by body

191   condition by adding residuals of mass prior to fledging (g) to the fixed-effect structure of the

192   model. For every model, we included the timing (Julian date) and duration (days) of the

193   preceding phase. To disentangle pre-exchange contexts (nestling origin) from post-exchange

194   contexts (rearing environment), we included the identity of both, the original and the fostering

195   pair as two random intercepts in all models. Thus, exchanged nestlings showed different pair

196   identities for the two contexts while unexchanged nestling showed the same pair identities.

197   We also included year as a random intercept to control for year-to-year variations.

198   **3. Results**

199   **(a) General patterns of dispersal**

200   We radio-tracked 160 little owl fledglings surviving to the first exploratory foray during the

201   pre-dispersal exploratory phase and dispersal transfer until first settlement, or until they died

202   or we lost contact with them. Sample sizes at the first foray until emigration was 67 fledglings

203   from 26 supplemented broods (36 females, 31 males), and 93 fledglings from 47

204   unsupplemented broods (55 females, 38 males). In this sample of surviving juveniles, we found

205   no significant relationship between body mass residuals at fledging and food supplementation

206   (β = 1.9; 95% CrI [-2.5, 6.3], n = 152), or body mass residuals and habitat suitability (β = -3.6;

207   95% CrI [- 22.2, 16.9], n = 152). After permanent emigration, 71 individuals did not complete

208   the transfer (we lost contact with 47 individuals, and 24 were found dead). We calculated

209   transfer duration and dispersal distance in the remaining 89 individuals from 20 supplemented

210   broods (22 females, 17 males), and from 33 unsupplemented broods (30 females, 20 males).

211   The variation of hatching date was comparatively small and most hatching occurred within a

212   month. Although the variability in the timing increased from hatching via fledging to dispersal

213   events, a major proportion of the population reached each event within a narrow time

214   window of c. 50 days (Fig. 1). Characteristics of the dispersal phases in the population are

215   presented in Table 1.

216   **(b) Exploratory forays**

217   We found a significant interaction between the food supplementation treatment and the

218   average habitat suitability index of the natal range in predicting the timing of first foray. In

219   poor habitats, supplemented individuals emigrated out of their natal range 22 days later than

220   unsupplemented individuals (Fig. 2). In contrast, in rich habitats, supplemented and

221   unsupplemented individuals started exploratory forays at about the same age (85 days old).

222   Unsupplemented fledglings (n = 93) tended to conduct forays later in rich habitats than in poor

223   habitats (β = 1.706; 95% CrI [-0.595, 4.167]). No other fixed-effect control variable influenced

224   the age of first foray (Table 2). Contrary to age at first foray, foray duration was not associated

225   with experimental food supplementation or habitat suitability, and none of the control fixed-

226   effect variable was an important predictor of foray duration (Table 2).

227   **(c) Emigration and transfer**

228   The age at emigration was positively related to both the age at first foray and the foray

229   duration (Table 2). Emigration was postponed by one day for each day an individual started

230   the exploratory phase later. Emigration was postponed by another day for each day the

231   exploratory phase lasted longer. Age at emigration also correlated positively with hatching

232   date (Table 2), indicating that the duration of the stages from hatching to emigration was

233   stable, modulated by factors affecting the start of exploratory forays. Duration of transfer was

234   not related to any of the focal or control variables (Table 3, Table S3). Finally, females (10.6 ±

11

235　　8.4 km) tended to disperse farther than males (7.1 ± 7.6 km; β = 0.584; 95% CrI [-0.557, 1.658];

236　　Table 3; Fig. S4).

237　　**(d) Pre-exchange versus post-exchange effects**

238　　We found that the explained variance in the age at first foray was 4.1 times higher for the

239　　nestlings' rearing environment after the exchange than for the shared origin before the

240　　exchange (Table 4). The variance ratio was 2.6 for foray duration, and 3.1 for age at

241　　emigration. These variance ratios show that juveniles sharing the rearing environment after

242　　the exchange were more similar in the age at first foray, duration of forays, and age at

243　　emigration than juveniles sharing the same origin before the exchange. Conversely, the

244　　rearing/origin variance ratios were 0.4 and 0.3 for transfer duration and dispersal distance,

245　　respectively (Table 4). Therefore, in dispersal characteristics following emigration the

246　　explained variance of shared origin before the exchange was 2.3 and 3.9 times higher than the

247　　explained variance of shared rearing environment after the exchange. Relative to the

248　　variances of shared origin before and rearing environment after the exchange, the year-to-

249　　year variance was larger for the duration of exploratory forays and transfer than for the timing

250　　events of foray start and permanent emigration (Table 4). In summary, individual dispersal

251　　behaviour until emigration was mainly determined by the nestlings' rearing environment

252　　rather than by the nestlings' origin. Conversely, post-emigration dispersal characteristics were

253　　mainly determined by the nestlings' origin.

254　　**4. Discussion**

255　　Our experiments enabled to disentangle various determinants of natal dispersal

256　　characteristics in little owls and support the hypothesis that juveniles delay dispersal when

257 food is abundant in the natal patch (i.e., delayed emigration hypothesis). First, food supply to

258 the growing juveniles was an important determinant of the timing of emigration: in low-

259 quality habitats, experimentally supplemented juveniles explored and emigrated later than

260 unsupplemented juveniles. This relationship disappeared in food-rich habitats where

261 unsupplemented juveniles also dispersed later, and thus at the same time as food

262 supplemented individuals. Natural variation in habitat quality had a similar effect on timing of

263 forays and emigration as had the experimental increase in food supply . Second, in addition to

264 the food supplementation, the effect of the shared rearing environment on timing of forays

265 and emigration was stronger than the effect of the shared origin. Conversely, shared origin of

266 the birds was an important determinant of the duration and the distance of the transfer phase.

267 Thus, after permanent emigration from the natal home range, innate individual factors

268 associated with their origin mainly affected the transfer phase. These results therefore

269 provide empirical support for theoretical considerations that causal factors strongly differ in

270 their effect on successive dispersal phases [14].

271 **(a) Effects of food supply**

272 Food supplementation and high habitat suitability of the natal home range delayed the timing

273 of first forays which carried over to a delayed timing of permanent emigration. This indicates

274 that the quality of the breeding home range affects not only the nestlings' growth and fledging

275 condition [30], but also the later development and behaviour until family break-up and

276 emigration of the juveniles. We therefore experimentally identified food resources during

277 rearing to be a main habitat factor modulating the timing of emigration. The fact that

278 increasing habitat suitability also delayed exploration behaviour in unsupplemented

279 individuals provides further correlative support, since habitat suitability is associated with

280 food availability and breeding success [31]. Strategies of delaying dispersal under food-rich

281 conditions have been shown to increase survival or inclusive fitness [32,33,50]. More

282 abundant resources within the home range could reduce competition among parents or

283 siblings, and thus, promote delayed dispersal [32,33]. In accordance with their own life-history

284 trade-offs the resident parents can stop parental care and thus, influence the emigration of

285 offspring [51,52]. Earlier termination of parental care or tolerance in food-poor home range

286 can improve the energetic conditions for the parents themselves [52]. Moreover, another

287 non-exclusive mechanism could explain the pattern of advanced dispersal in food-poor

288 habitats: early emigration from poor patches may enable individuals to find better conditions

289 early. This in turn could increase their fitness, in particular if dispersers from food-poor home

290 ranges can settle earlier than better-fed competitors [38,39].

291 **(b) Other fostering environment effects**

292 As in studies investigating the natal dispersal of eagle owls (*Bubo bubo*) [53,54], we found a

293 stronger effect of the shared rearing environment than of the shared nestling origin on timing

294 of emigration. However, our study controlled for the effects of food supplementation and

295 habitat suitability in the natal habitat. Thus, the importance of the shared rearing environment

296 for early phases of dispersal in our study suggests that other environmental factors than food

297 availability also affect dispersal timing and the duration of the exploratory phase. Two possible

298 non-exclusive mechanisms operating in the rearing environment can explain this effect. First,

299 essential features of the habitat that were not captured by our habitat suitability model could

300 influence timing of emigration, e.g. micro-structures affecting resource availability or

301 mortality risk such as roost sites [41], food accessibility [40] or predator occurrence [55] during

302   the post-fledging period. Second, the social context, including parental or sib-sib aggression,

303   might have been important in affecting emigration timing [24,56,57].

304   **(c) Importance of origin versus rearing environment**

305   We disentangled the effects of a shared origin (before exchange) from the effects of the

306   shared rearing environment (after exchange) using a partial cross-fostering experiment. We

307   found that the timing of first forays and of emigration was determined by the rearing

308   environment rather than by origin. In contrast, the shared origin was the more important

309   determinant of the duration of the transfer phase and the distance dispersed. The effect of

310   origin on dispersal behaviour can develop by different mechanisms: either the behaviour is

311   determined genetically [19,20,58], affected by prenatal maternal effects [12], or by

312   environmental effects transferred to offspring epigenetically [21]. However, since cross-

313   fostering was not conducted at hatching, we cannot exclude that the effect of origin partly

314   developed due to a shared environment early in the nestling period. Our results show that, as

315   dispersal advanced, the importance of the rearing environment decreased while the

316   importance of origin increased. The effects of the rearing environment affecting pre-

317   emigration dispersal phases did not carry-over to the transfer phase. We therefore suggest

318   that the transfer phase, i.e. the movement part of dispersal resulting in spatial dynamics

319   within and between populations, is only marginally driven by the conditions juveniles

320   experienced in the natal home range and more by innate dispersal phenotypes and conditions

321   encountered during the transfer phase when moving around within and between populations.

322   The duration of the exploration and the transfer phase showed large between-year

323   differences, potentially due to year-specific differences encountered during explorations or

324   transfer such as food availability [40], fluctuations in conspecific densities [23,25], or annual

325 climatic variations [59]. Moreover, it is likely that transfer duration and distance are strongly

326 influenced by the broader landscape conditions encountered post-emigration. We have

327 shown elsewhere that suitable habitat influences little owl movement trajectories during

328 dispersal [60]. Thus, strong effects operating during the transfer phase might even hide carry-

329 over effects from the pre-emigration phase. This is consistent with the idea of the broader

330 landscape and habitat encountered on the move being the main factor affecting natal

331 dispersal trajectories during the transfer phase [14,22,48].

332 **5. Conclusion**

333 We found limited evidence that innate traits play an important role for the timing of

334 emigration. We suggest that the proximate causes affecting emigration are likely in the

335 context of the natal habitat conditions and the social environment. However, determinants

336 related to the juveniles' origin and innate traits appeared to shape the dispersal behaviour

337 during transfer and settlement. Our results therefore suggest that the timing of obligate natal

338 dispersal movements in little owls is extrinsically affected by the rearing environment. In

339 contrast, the duration and distance of natal dispersal depends more on intrinsic factors

340 associated with origin, and with sex being a predictor of dispersal distance. A lack of

341 association between timing of emigration, and duration and distance of transfer indicates a

342 breakdown of initial behavioral correlations as the process advances [61]. Pre-emigration and

343 post-emigration dispersal behaviours related each to a different suite of pre-emigration

344 correlates [62]. Thus, causal factors differed greatly in their effect on different dispersal

345 phases. This suggests that optimal timing and optimal duration of dispersal represent life-

346 history traits that may have evolved independently. While the ultimate causes for the habitat-

347 dependent timing of emigration might be kin competition within the natal home range, the

348 ultimate causes for dispersal duration and distance are likely associated with the spatio-

349 temporal variation in habitat quality and its interaction with population density outside of the

350 parental home range. Such dispersal pattern likely occurs in species with year-round

351 territories where juveniles do not explore the surroundings of their parental home ranges

352 during the post-fledging period, and have to share resources with their kin, but do not gain

353 any information about quality of the broader habitat or population density before dispersal.

354 **DATA ACCESSIBILITY**

355 The primary telemetry and dispersal parameters data have been submitted as Electronic

356 Supplementary Material.

357 **AUTHORS' CONTRIBUTIONS**

358 BND and MUG conceived the ideas and designed methodology; MP, BND and MUG collected

359 the data; JF and MP analysed the data; JF and MUG led the writing of the manuscript. All

360 authors contributed critically to the drafts and gave final approval for publication.

361 **COMPETING INTERESTS**

362 We have no competing interests

363 **FUNDING**

366 **ACKNOWLEDGEMENTS**

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546   Table 1. Sample size, mean and range of individual traits and natal dispersal characteristics in

547   little owl fledglings.

Variable	N	Mean ± SD	Median [range]
Hatching date (Julian day)	160	141[a] ± 10	140[b] [125 – 183]
Habitat suitability index	160	0.85 ± 0.12	0.86 [0.55 – 1.00]
Age of first foray (day)	160	85.2 ± 19.4	86 [30 – 129]
Foray duration (day)	160	28.3 ± 35.9	19 [0 – 195]
Age of emigration (day)	160	112.9 ± 42.7	109 [26 – 310]
Transfer duration (day)	89	22.6 ± 32.6	10 [1 – 175]
Net dispersal distance (km)	89	9.7 ± 7.3	7.6 [0.5 – 30.8]

548   [a]May 21 ± 10 days; [b]May 20 [May 5 – July 2]

Table 2. Fixed and random coefficients and credibility intervals of generalized linear mixed-models investigating factors affecting (i) age at first foray out of the natal range, (ii) foray duration, and (iii) age at emigration in 160 little owl fledglings. Coefficients with 95% credibility interval not overlapping zero are denoted significant effects.

Fixed-effect variables	Age at first foray[a]			Foray duration[b]			Age at emigration[c]		
	β	Lower 95% CrI	Upper 95% CrI	β	Lower 95% CrI	Upper 95% CrI	β	Lower 95% CrI	Upper 95% CrI
(Intercept)	13.468	9.317	17.638	-1.288	-13.349	10.927	3.181	1.972	4.401
Food-supplementation	3.099	0.128	6.036	0.446	-0.895	1.756	0.006	-0.128	0.138
Habitat suitability index (HSI)	-1.925	-4.615	0.888	-0.168	-5.163	4.986	-0.047	-0.564	0.452

Food-supplementation X HSI	-3.423	-6.801	-0.015	-	-	-	-	-	-
Males	0.131	-0.183	0.443	0.312	-0.648	1.264	-0.068	-0.17	0.03
Hatching date	-0.019	-0.042	0.005	0.037	-0.034	0.108	0.009	0.002	0.016
Age at first foray	-	-	-	0.012	-0.016	0.04	0.058	0.055	0.06
Foray duration	-	-	-	-	-	-	0.042	0.04	0.043

552 [a] Random-effect variance [95% credibility interval]: pre-exchange 0.101 [0.000, 0.457]; post-exchange 0.419 [0.028, 0.880]; year 0.200 [0.000, 1.330]

553 [b] Random-effect variance [95% credibility interval]: pre-exchange 1.265 [0.002, 4.614]; post-exchange 2.591 [0.031, 6.462]; year 4.328 [0.021, 26.175]

554 [c] Random-effect variance [95% credibility interval]: pre-exchange 0.008 [0.000, 0.033]; post-exchange 0.034 [0.006, 0.068]; year 0.028 [0.000, 0.420]

555 Table 3. Fixed and random coefficients and credibility intervals of generalized linear mixed-models investigating factors affecting (i) transfer

556 duration, and (ii) net dispersal distance in 89 little owl fledglings. Coefficients with 95% credibility interval not overlapping zero are denoted

557 significant effects.

	Transfer duration[a]			Net dispersal distance[b]		
Fixed-effect variables	**β**	**Lower 95% CrI**	**Upper 95% CrI**	**β**	**Lower 95% CrI**	**Upper 95% CrI**
(Intercept)	-1.401	-12.504	9.244	4.06	-1.521	9.426
Food supplementation	0.596	-0.491	1.707	0.102	-0.419	0.613
Habitat suitability index (HSI)	-0.666	-5.384	3.929	-0.26	-2.483	1.992
Males	0.268	-0.788	1.285	-0.429	-0.943	0.079
Hatching date	0.046	-0.021	0.112	-0.006	-0.038	0.028

Age at emigration	-0.003	-0.029	0.022	-0.001	-0.012	0.011
Transfer duration	-	-	-	0.004	-0.003	0.012

558   [a] Random-effect variance [95% credibility interval]: pre-exchange 0.724 [002, 2.712]; post-exchange 0.277 [0.000, 1.288]; year 2.045 [0.007, 13.051]

559   [b] Random-effect variance [95% credibility interval]: pre-exchange 0.235 [0.001, 0. 699]; post-exchange 0. 098 [0.000, 0. 0.441]; year 0.260 [0.000, 1.870]

560   Table 4. Random-effect variance and credibility intervals of generalized linear mixed-models

561   with identical additive fixed-effect structure for comparison of their relative importance

562   during dispersal of little owl fledglings. Sample sizes for each dispersal stage are indicated.

Model	Random-effect variables	Variance	Lower 95% CrI	Upper 95% CrI
Age at first foray (n =160)				
	Pre-exchange	0.101	0.000	0.457
	Post-exchange	0.419	0.028	0.880
	Year	0.200	0.000	1.330
Foray duration (n = 160)				
	Pre- exchange	1.131	0.003	4.435
	Post- exchange	2.963	0.049	6.835
	Year	4.414	0.028	25.795
Age at emigration (n= 160)				
	Pre- exchange	0.471	0.001	1.634
	Post- exchange	1.476	0.250	2.986
	Year	1.144	0.002	6.871

| **Transfer duration (n = 89)**				
	Pre- exchange	0.656	0.001	2.641
	Post- exchange	0.284	0.000	1.382
	Year	2.275	0.009	13.619
Net dispersal distance (n = 89)				
	Pre- exchange	0.304	0.002	0.800
	Post- exchange	0.077	0.000	0.372
	Year	0.255	0.000	1.751

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564

565   **FIGURE CAPTIONS**

566   Figure 1 – Density distribution of hatching date (black), date of first foray (darkest grey), date

567   of emigration (grey), and date of first settlement (lightest grey) in little owl fledglings. The

568   vertical dashed lines of corresponding grey shading indicate the mean value for each event.

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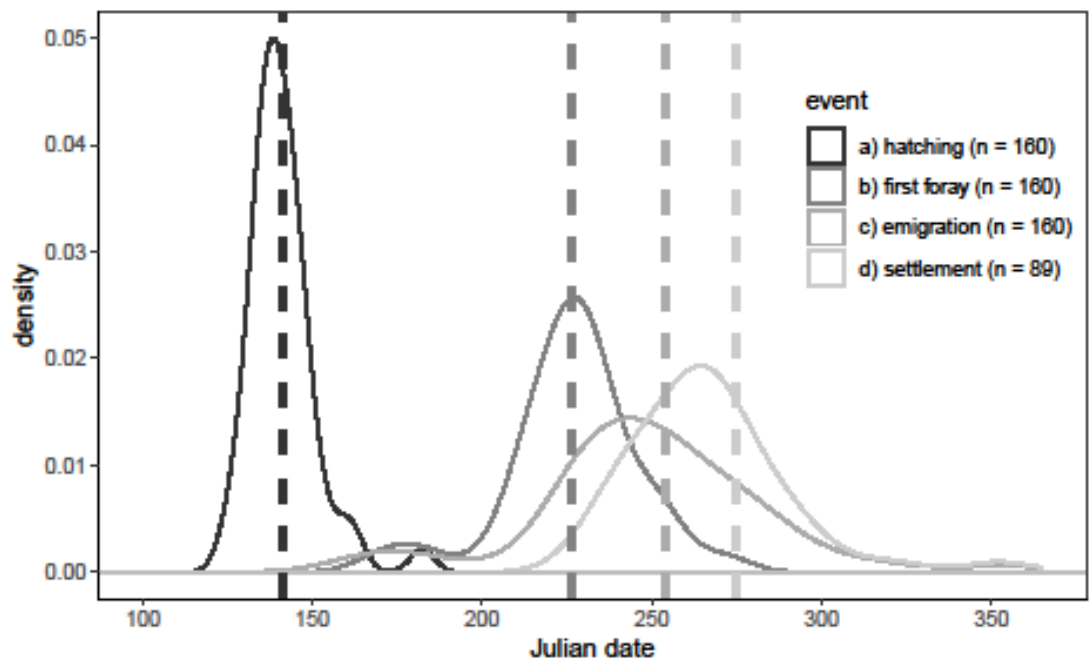
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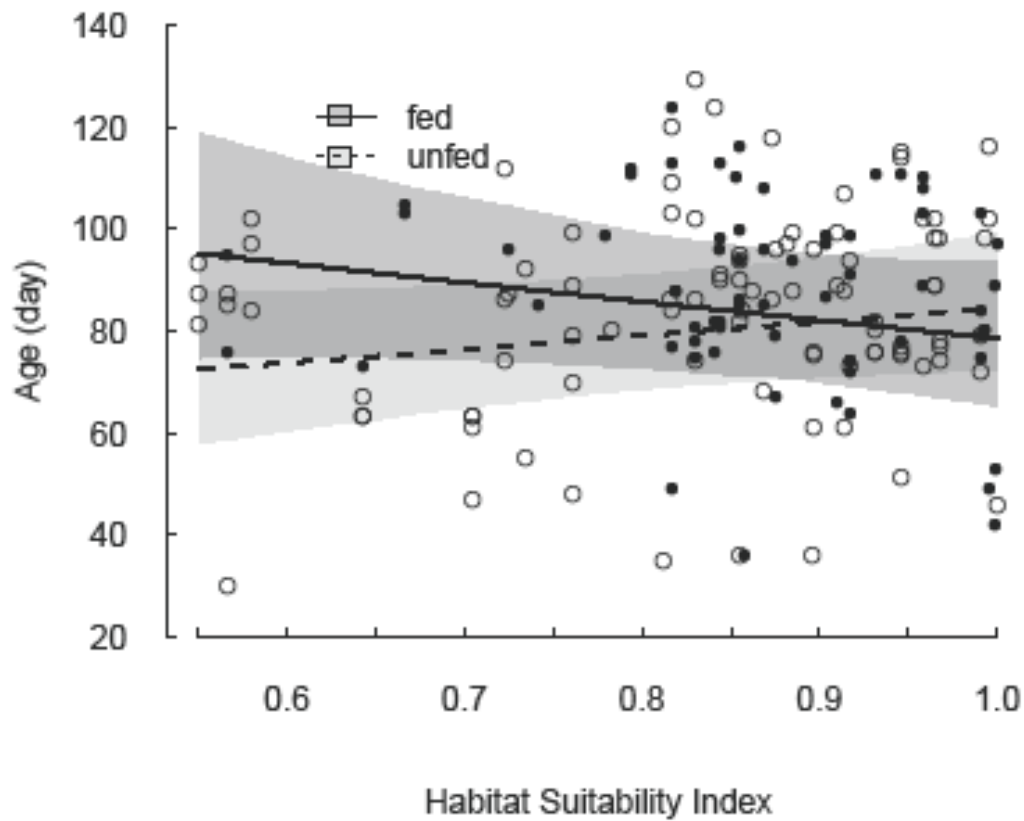
573

574 Figure 2 – Predicted age at first foray in relation to habitat suitability for 67 little owl fledglings

575 from 26 food-supplemented broods (black dots, solid line, 95% CrI dark grey shaded area),

576 and 93 fledglings 47 unsupplemented broods (open circles, broken line, 95% CrI light grey

577 shaded area).