

RESEARCH ARTICLE

Sex and size shape the ontogeny of partial migration

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Abstract

1. The arrival-time hypothesis of partial seasonal migration proposes that overwinter residence is driven by reproductive benefits of early presence on the breeding grounds. Thus, it predicts increased occurrence of residence at reproductive age. In contrast, the body size hypothesis proposes age-independent benefits of residence for large individuals, who should exhibit greater winter tolerance. Despite different expectations in age patterns for the two hypotheses in long-lived partially migrant species, there is little empirical work investigating the ontogeny of migratory phenotypic expression, that is the expression of residence or migration.
2. We investigated the influence of age, sex and body size on migratory phenotype throughout ontogeny (from first year to early adulthood) in a long-lived partially migrant species, the red kite *Milvus milvus*. We GPS-tracked 311 individuals tagged as juveniles and 70 individuals tagged as adults over multiple years, yielding 881 observed annual cycles. From this data, we estimated age-dependent probabilities of the transition to residence and of survival in migrants and residents using a Bayesian multistate capture-recapture model, as well as the probability of resuming migration once resident. We then calculated the resulting proportion of residents per age class.
3. In both sexes, almost all juveniles migrated in their first winter, after which the probability of becoming resident gradually increased with age class to approximately 0.3 in adults (>3 calendar years). A size effect in third calendar year females suggests that large females adopt residence earlier in life than small females. The transition from residence back to migration only occurred with a probability of 0.15 across all resident individuals. In addition, survival was notably reduced in adult male migrants compared to adult male residents. These results are largely consistent with the arrival-time and body size hypotheses, simultaneously.
4. Our results reveal a plastic, yet primarily directional within-individual change in migratory phenotype towards more residence with increasing age, varying between sexes and between individuals of different size. This study highlights that different individual characteristics can jointly shape the ontogeny of migratory

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behaviour and result in complex within-population patterns and persistence of migratory phenotypes.

KEYWORDS

condition-dependence, life-history transition, migratory phenotype, migratory plasticity, *Milvus milvus*, raptor, red kite

1 | INTRODUCTION

Migration, defined here as a seasonal round-trip movement between breeding and non-breeding areas, is driven by the need to cope with fluctuating resource availability and conditions in seasonal environments (Denryter et al., 2022; Somveille et al., 2015). However, in some migratory populations, the propensity to migrate can vary between individuals, such that both migrants and year-round residents co-exist; this is known as partial migration (Lack, 1944; Terrill & Able, 1988). Partial migration can occur due to both fixed and changing migratory phenotypes within individuals, arising from genetic variation and plasticity (Berg et al., 2019; Lundberg, 1987; Pulido, 2011). This variation may be influenced by factors such as early-life environments, condition-dependence and density-dependence. In this study, we are interested in investigating how variation in migratory behaviour arises within and among individuals.

Mechanisms influencing migratory phenotypic expression are commonly believed to be adaptive and shaped by a maximisation of fitness in terms of survival and/or reproduction. This, in turn, can be influenced by individual characteristics. These characteristics can be fixed or variable, such as age, sex, body size or body condition, and their resulting association with migratory phenotypic expression is often termed "condition-dependence" (Berg et al., 2019; Chapman et al., 2011; Lundberg, 1987). Partially migrant systems exhibiting within-individual phenotypic plasticity provide a particularly exciting opportunity to study individual-specific trade-offs regarding migratory behaviour, as well as the resulting population-level consequences.

Several hypotheses outline potential factors underlying condition-dependent migratory behaviour (reviewed in Berg et al., 2019; Chapman et al., 2011). These hypotheses rely on the assumption that migration maximises the expected fitness of individuals due to seasonal environmental deterioration in the breeding area (Somveille et al., 2015) resulting in reduced survival or poor pre-breeding body condition in residents (Acker, Daunt, et al., 2021; Fryxell & Sinclair, 1988; Harrison et al., 2011). However, the arrival-time hypothesis (ATH; Ketterson & Nolan, 1976, 1983) proposes that residents (or early arriving migrants) will have first choice of breeding habitats (Kokko, 2011), and according to the ideal despotic distribution, likely acquire the high-quality breeding territories (Fretwell & Lucas, 1969; Sergio & Newton, 2003). Additionally, residents may have heightened resource-holding potential when migrants return and attempt to usurp territories (theory of prior residency; Forstmeier, 2002; Jakobsson, 1988; Kokko, 2011). These

factors may allow residents to better establish and defend high quality territories, and initiate breeding earlier than migrants (Bennett et al., 2022; Kokko, 1999, 2011). Therefore, under the ATH, sexually mature individuals and the sex responsible for territory acquisition are expected to benefit more from residence than sub-adults or the mate-choosing sex and are predicted to have a higher probability of residence (Boyle, 2008; Marques et al., 2010; Morbey & Ydenberg, 2001).

According to the body size hypothesis (BSH; Ketterson & Nolan, 1976), larger individuals should have allometrically enhanced thermoregulatory capacity and fat storage compared to smaller individuals. Therefore, under the BSH, large individuals should be better able to cope with adverse environmental conditions in the breeding area over winter than small individuals and should have a higher probability of residence (Boyle, 2008; Chapman et al., 2011; Jahn et al., 2010; Ketterson & Nolan, 1976). Additionally, large individuals likely have a competitive advantage over small individuals (Marra, 2000; Piper et al., 2000; Richner, 1989), which could be particularly important for the acquisition of scarce winter food resources (social dominance hypothesis; Gauthreaux, 1982). While the factors underlying the size effect—thermal tolerance, fasting endurance and social dominance—are often split into different hypotheses, due to their confounding relationship we consider them together under the BSH.

Though multiple factors may simultaneously affect migratory phenotype, combined effects have rarely been investigated (but see Jahn et al., 2010; Ketterson & Nolan, 1983). Furthermore, while evidence of age-dependent migratory behaviour has been found in both partial and full migrant populations, manifesting as differences in migratory phenotype versus timing/distance, respectively (Bai et al., 2012; Boyle, 2008; Campioni et al., 2020), it remains unclear how the importance of factors influencing migratory behaviour change throughout an individual's ontogeny. This is particularly interesting in long-lived species, in which breeding recruitment may be delayed beyond sexual maturity (Becker et al., 2008; Fay et al., 2016; Sergio et al., 2017), enabling a comparison of the effects of fixed characteristics with those of ontogenetic processes on the migratory phenotype. However, few studies have been able to follow enough individuals for long enough to quantify the entire variation of individual characteristics and migratory phenotypes across a species' ontogeny (Hebblewhite & Haydon, 2010; Senner et al., 2020).

In this study, we aimed to investigate the effects of individual characteristics on migratory phenotypic expression across an animal's ontogeny, from the first calendar year (1CY) to early adulthood.

We used GPS tracks from a partially migrant population of red kites *Milvus milvus* to derive longitudinal data on migratory phenotype and survival. By using these data in combination with known individual characteristics, we could examine the potential interactive occurrence of factors underlying the ATH and the BSH and how the importance of individual characteristics changed with age. In red kites, individuals may delay breeding beyond sexual maturity (2CY; Aebischer & Scherler, 2021). Therefore, we used age as a proxy for breeding probability, with the expectation that older birds will exhibit a higher probability of residence (Figure 1a). Furthermore, as males are often the territory-establishing sex in birds (Greenwood, 1980), we expected a higher probability of residence in males compared to females. In addition, we expected that the benefits of body size predicted by the BSH (Figure 1b) could act additively or interactively with an effect of age (Figure 1c,d, respectively). This could cause deviation in the age of the possible transition to residence from the age of sexual maturity. Finally, both the ATH and BSH operate under the assumption that residence has a negative effect on survival, explaining why a benefit in the form of enhanced reproduction would be necessary to outweigh the costs of overwintering in the breeding area, and why individuals that are physically less vulnerable to harsh winter conditions would be more likely to be resident. Therefore, we also expect to see lower survival in residents than migrants, in general. By examining the role of individual characteristics in the

expression of migratory phenotypes, as well as potential effects of migratory phenotypes on survival, we contribute novel insights to the growing body of literature examining the form and magnitude of phenotypic plasticity in migratory behaviour in animal populations.

2 | MATERIALS AND METHODS

2.1 | Study species and area

The red kite is a long-lived partially migrant raptor occurring throughout much of Europe. In contrast to other parts of their distribution range, the population size in Switzerland has been increasing for approximately 40 years, from an estimated 150 breeding pairs in 1976 to around 3500 breeding pairs in 2016 (Aebischer & Scherler, 2021; Knaus et al., 2018; Schifferli et al., 1980). Migrants from the Swiss population spend the non-breeding period in France, Spain or Portugal. The first evidence of a red kite overwintering in Switzerland was documented in 1961 (Zimmermann & Sutter, 1962) and the occurrence of this phenomenon has substantially increased in the last decades, with 3000–5000 red kites (of unknown origin), observed at winter roosts across the country in winter 2020/2021 (Aebischer & Scherler, 2021). Our study area is located in western Switzerland, in the Cantons of Fribourg and Berne (centroid: 7.26749E, 46.80188N EPSG:4326), covering 387 km² and ranging from 482 to 1763 m.a.s.l. (for details see Nägeli et al., 2022; Welti et al., 2020). This breeding population is part of a high-density region of red kites, with as many as 30 breeding pairs per 100 km² (Knaus et al., 2018), among the highest breeding densities recorded. Breeding territoriality in red kites reinforces the potential importance of residence for territory acquisition and holding. Furthermore, despite an elevation difference of almost 600 m between some nest-sites in our population, mean nest-site elevations of migrants and residents do not differ (mean_{migrant} = 765 m.a.s.l., range_{migrant} = 503–1050 m.a.s.l.; mean_{resident} = 748 m.a.s.l., range_{resident} = 519–1087 m.a.s.l.; Witczak, 2023). This indicates that harsher overwinter conditions at higher elevations do not sufficiently alter the energetic requirements of individuals to favour a particular migratory phenotype. In addition, within the study population, home ranges do not shift substantially from the breeding to non-breeding season in residents (Nehm, 2020), suggesting that staying near the territory year-round holds greater benefits than extensive ranging behaviour in winter, even in high-elevation habitats.

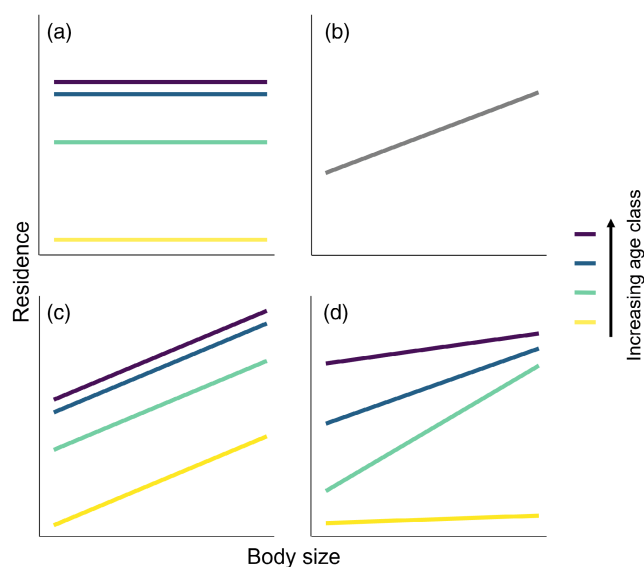


FIGURE 1 Age class and body size effects on residence, predicted by the arrival-time and body size hypotheses. (a) Arrival-time hypothesis: Older individuals are more likely to be resident than younger individuals, independent of size. (b) Body size hypothesis: Increasing body size results in a higher probability to be resident, independent of age. (c) Additive combination of the arrival-time and body size hypotheses: Older individuals are more likely to be resident than younger individuals, modulated similarly in each age class by body size. (d) Interactive combination of the arrival-time and body size hypotheses: Older individuals are more likely to be resident than younger individuals, modulated differently in each age class by body size.

2.2 | Capture, logger-fitting and individual characteristics

We captured both nestling and breeding red kites and fit them with GPS loggers. Nestlings were caught by a tree climber just prior to fledging (35–45 days post-hatching). We avoided climbing after chicks were 45 days old to prevent premature fledging. Adults were caught using a Dho-Gaza net and a live decoy predator (Eurasian

eagle-owl *Bubo bubo*; details in Witczak, 2023). For each captured bird, we measured tarsus length (mm), a commonly used proxy for avian body size (e.g. Baladrón et al., 2015; Schaadt & Bird, 1993), and took a blood sample for genetic sexing. Tarsus length stabilised well before the end of the nestling period and was, therefore, assumed to remain fixed across ontogeny. We calculated a body size index using tarsus length centred on each ringer's mean to account for observer bias. Additionally, we centred those values on the sex means due to a marginal reverse sexual dimorphism in red kites (Aebischer & Scherler, 2021; tarsus lengths: mean_{female} = 60.80 mm, range_{female} = 49.0–69.3 mm, n_{female} = 188; mean_{male} = 59.82, range_{male} = 47.80–71.00, n_{male} = 193; see Supporting Information Figure S1.1 for population body size distribution). When presenting model predictions for body size, we de-centred sizes per sex and used the tarsus length mean of the most common ringer. Sex was determined genetically using the CHD1 sex chromosome (details in Fridolfsson & Ellegren, 1999; Nägeli et al., 2022). Our assumptions regarding fixed body size and sex do not apply to all partially migrant systems. Therefore, it is advisable to use caution when applying our interpretations in the context of other species and taxa (e.g. size in amphibians: Hurlbert, 1970; and in fish: Futamura et al., 2022; sex in fish: Higgins et al., 2015).

We fit nestlings and breeding birds with solar-powered GPS-GSM-UHF loggers (SKUA/CREX type, Ecotone Telemetry, Gdynia, Poland and GsmRadioTag-M9 type, Milsar, Cluj Napoca, Romania) using a backpack-style diagonal-loop harness (Kenward, 1985; Meyburg & Fuller, 2007; for additional details, see Scherler, Witczak, et al., 2023). Loggers and harness weighed maximally 3.17% of the body weight of the lightest adult red kite caught. GPS data from the loggers were transmitted using GSM, 2G or 3G networks, and were subsequently saved on and managed through Movebank (Wikelski et al., 2021). Ringing and tagging were permitted by the Canton of Fribourg Amt für Lebensmittelsicherheit und Veterinärwesen (Permit No. 2015_13_FR and 2017_29_FR) and the Swiss Federal Office for the Environment.

In birds caught as nestlings, we knew the exact age. In birds caught as breeding adults, it is not possible to determine exact age beyond 3CY. However, given that the earliest recruitment observed in our population occurred in the 3CY, we created four age classes: 1CY, 2CY, 3CY and adult (>3CY) in order to distinguish between birds known to be 3CY, and those likely to be older.

Migratory phenotype was determined following the expert-based approach described in Scherler (2020). This approach combines (a) plotting the daily mean displacement of GPS points in relation to the location during the breeding season with (b) visual verification of the GPS points on a map for spatial context. A detailed description can be found in Supporting Information S1.2, Figure S1.2.

2.3 | Statistical analyses

We summarised data from each individual in a migration history, which is a vector with length corresponding to the number of study

years, and vector elements (hereafter “states”) corresponding to the current migratory phenotype and mortality status ($n=5$; alive migrant, alive resident, dead migrant, dead resident, dead unknown phenotype). Migration histories were modelled using a multistate capture-recapture model with perfect detection and state uncertainty implemented in JAGS 4.3.0 (Plummer, 2003), interfaced from R 4.0.2 (R Core Team, 2020) via RStudio 1.3.959 (RStudio Team, 2020) and using the package jagsUI 1.5.1 (Kellner, 2019). The model estimates the probabilities of a migrant becoming a resident and vice versa, as well as state-specific survival. The transition from migrant to resident was modelled by an interaction between age class, sex and body size. Due to the rarity of the resumption of migration once resident, the transition from resident to migrant was estimated as a constant across all individuals. Likewise, due to the rarity of residence in the 1CY, we estimated mean probabilities of migration or residence across all individuals of this age class. Survival was modelled by an interaction between age class, sex and migratory phenotype. We used vague priors (uniform distribution, or normal distribution where the transition probability was logit-transformed) for all parameters and ran Markov chains to convergence based on $\hat{R} < 1.1$. We excluded two individuals with data gaps in more than 1 year and assumed detection probability to be 1. Individual-level, year and cohort effects were not accounted for in the model, due to a data imbalance in age classes across the study years. See Supporting Information S1.3 for a full description of the modelling approach and Supporting Information S2 for the code.

We calculated the expected proportion of residents at each age by simulating a population process adapted from population models (Schaub & Kéry, 2021). For this simulation we initiated a hypothetical population with 500 male and 500 female fledglings and calculated the number of surviving birds at each subsequent age by taking random binomial draws based on the survival and transition probabilities estimated by our model for each age class, sex, and body size (we used ‘adult’ estimates for all ages >3CY). This resulted in the total number of migrant and resident individuals still alive by each age and sex for each body size. We then calculated the proportion of residents per age, sex and body size, and summarised the proportion of residents across all body sizes and MCMC samples to present proportions for ages and sexes. In order to determine whether/when an asymptote was reached in the proportion of residents, we specified the process for 20 age-classes, and found that the proportion of residents did not change anymore (<1% increase in proportion of residents between subsequent age-classes) after males and females reached approximately 10 and 11CY, respectively. See Supporting Information Figure S1.4 for sex-specific asymptote curves and S2 for annotated code showing how the proportion of residents was calculated.

We report the posterior mean and 95% credible intervals (denoted: CrI or using []) as measures of uncertainty for all parameter estimates. To assess whether two given groups differed in their transition probabilities or survival, we extracted the proportion of posterior samples where values of one group were greater than values of the other group, and report these as posterior probabilities

(PP) of a pairwise difference between those groups (Korner-Nievergelt et al., 2015). For the continuous variable body size, we compared groups at the 10% (small) and 90% (large) quantiles of the population body size distribution (females: small = 56.82 mm, large = 64.52 mm; males: small = 55.70 mm, large = 63.40 mm). For estimation of the age asymptote in the proportion of residents, body size was held constant at the mean (males: 59.82 mm; females: 60.80 mm).

Between 2015 and 2019, we fitted 424 red kites with GPS loggers, of which 346 were caught as nestlings and 78 were caught as breeding birds. Thirty individuals were removed due to early logger loss or failure resulting in no data, while an additional two birds were removed due to data gaps. A further 11 individuals were excluded due to missing sex or size parameters. This resulted in 381 birds with known migratory phenotype and survival states, totalling 881 annual events (mean = 2.31 events/bird, SD = 1.22, range = 1–5; see Supporting Information S1.5 for sample size details).

3 | RESULTS

Almost all 1CY individuals migrated, with an estimated probability of migration of 0.96 [0.93, 0.98]. The probability of switching to residence gradually increased with age (Figure 2), such that migrant

adults transitioned to residence with a probability of 0.32 [0.07, 0.70], while 1CY birds transitioned to residence with a probability of only 0.04 [0.02, 0.07] ($PP_{Ad > 1CY}$: 0.99). Once individuals became resident, the estimated probability of migrating was only 0.15 [0.10, 0.21], indicating that residents mainly remain resident. In the 3CY, the probability of transitioning to residence was higher in large (0.19 [0.06, 0.39]) than small females (0.006 [0.000004, 0.04]; $PP_{L > S}$: 0.997; Figure 2). This suggests that large females switch to residence younger than small females, as a larger proportion is predicted to have already transitioned to residence by the 3CY (Figure 3). These interactions between age class, sex and body size resulted in a largely age class-dependent but not size-dependent transition probability in males, and an interactive age class-dependent and size-dependent transition probability in females (Figure 3). See Supporting Information Table S1.6a for complete results on transition probabilities.

Monthly survival probability increased with age from 0.96 [0.95, 0.97] in the 1CY to 0.98 [0.96, 0.999] as adults ($PP_{Ad > 1CY}$: 0.98) among migrants and from 0.92 [0.69, 0.999] in the 1CY to 0.996 [0.99, 0.9999] as adults ($PP_{Ad > 1CY}$: 0.96) among residents. In particular, resident females seemed to have relatively low survival in the 1–2CY, albeit with very large uncertainty due to the low probability of residence in these age classes (Figure 4). Finally, the difference in survival between migrants and residents was particularly important in adult males, where migrants (0.97 [0.96, 0.99]) had lower survival

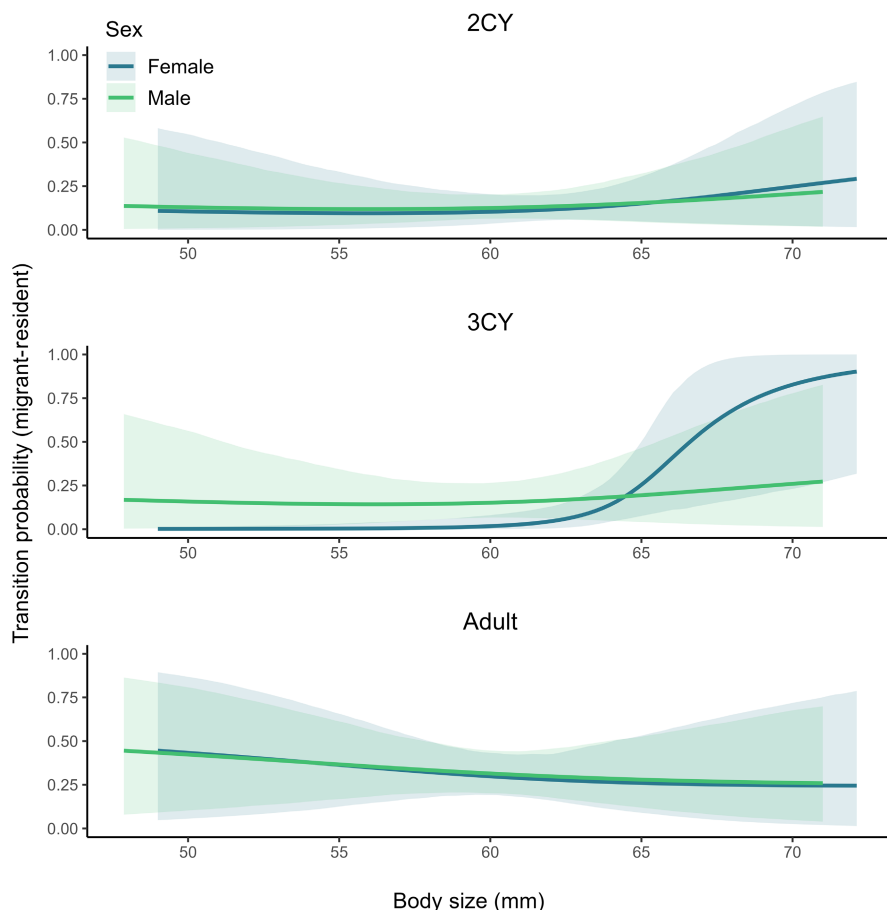


FIGURE 2 Mean ($\pm 95\%$ credible interval) annual transition probability of red kites from migrant to resident by age class (2CY, 3CY, Adult; CY = calendar year), sex (Female, Male) and body size. Body size was measured as tarsus length in mm.

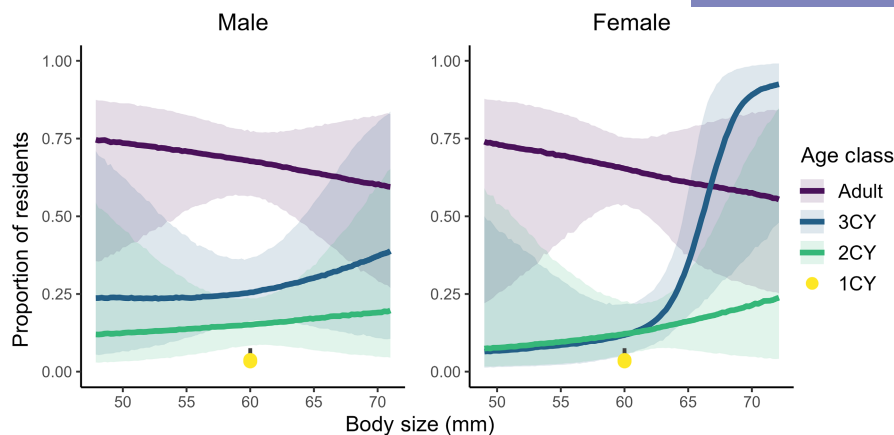
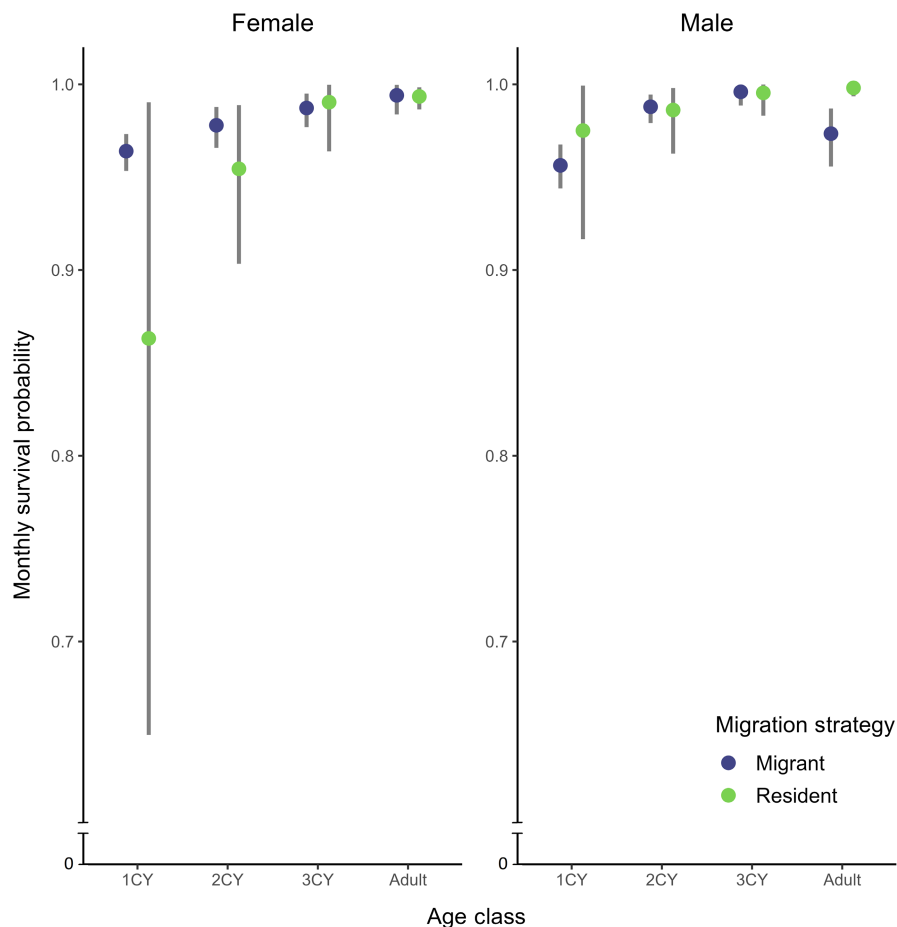


FIGURE 3 Mean ($\pm 95\%$ credible interval) proportion of resident red kites by age class (1CY, 2CY, 3CY, Adult; CY = calendar year), sex (Female, Male) and body size. Body size was measured as tarsus length in mm. The proportion of residents in the 1CY was calculated across all individuals; thus, a point with error bar shows the mean and credible interval for that age class. The proportion of residents presented for the adult age class corresponds to the age at which each sex reaches its asymptote (males: 10CY; females: 11CY).

FIGURE 4 Mean ($\pm 95\%$ credible interval) monthly survival probabilities of red kites with different migratory phenotypes (Migrant, Resident) by age class (1CY, 2CY, 3CY, Adult; CY = calendar year) and sex (Female, Male).



than residents (0.998 [0.99, 0.99995]; $PP_{M < R}$: 0.999; Figure 4). Annual survival probabilities ranged from 0.65 [0.56, 0.72] to 0.93 [0.82, 0.996] in female migrants, from 0.59 [0.50, 0.67] to 0.95 [0.87, 0.99] in male migrants, from 0.28 [0.006, 0.89] to 0.92 [0.85, 0.98] in female residents, and from 0.76 [0.35, 0.99] to 0.98 [0.93, 0.999] in male residents. See Supporting Information Table S1.6b and c for complete results on monthly and annual survival.

4 | DISCUSSION

By following a large sample of individuals over multiple years, we show that age, sex and body size can interactively shape within-individual variation in migratory phenotype in partially migrant populations. Red kites were almost exclusively migrant in the 1CY, but increasingly switched to residence thereafter. The switch to residence largely

occurred after sexual maturity (2CY; Aebischer & Scherler, 2021), near the earliest observed age of first reproduction in this population (3CY). Once resident, individuals rarely switched back to migrant, and adult males appeared to derive a substantial survival benefit from remaining resident, which might explain why red kites exhibit a directional switch towards residence. Furthermore, sex and body size modulated the age at which individuals transitioned to residence, with size important in 3CY females. Therefore, an interactive effect of factors underlying the ATH and BSH was associated with transition probability in females, while factors underlying the ATH were associated with transition probability in males. Consequently, our results are largely compatible with the ATH as an underlying mechanism of plastic migratory behaviour in this partially migrant species and suggest that the effect of size-related characteristics on migratory life-history trade-offs may be restricted to specific ontogenetic phases or sex-dependent roles. Furthermore, the largely directional nature of the transition to residence highlights that migratory phenotypic expression is not only a facultative response to inclement weather in this species, but an important life-history transition.

4.1 | Arrival-time hypothesis: Establishing and holding territories

As predicted by the ATH, we found that older birds were more likely to transition to residence than younger birds, suggesting that residence may hold reproductive benefits for sexually mature individuals. Similar patterns in migratory behaviour through ontogeny have been observed in other species of partial and full migrants (we expect that residence in partially migrant populations and early arrival in full migrant populations hold similar benefits for fitness; Campioni et al., 2020; Ogonowski & Conway, 2009; Snell et al., 2021; but see Fudickar et al., 2013). In contrast with predictions by the ATH, we found no evidence that male red kites have a higher probability to transition to residence than females. Indeed, a high probability of females becoming resident around the age of first reproduction suggests that residence also results in fitness benefits for females, and that benefits may be likewise reproductive in nature (e.g. mate-finding), possibly explaining this lack of difference. Finally, the largely directional switch from migrant to resident has also been observed in other species (Able & Belthoff, 1998; Ogonowski & Conway, 2009; Schwabl, 1983), though it is not universal (Hegemann et al., 2015; Reid et al., 2020).

While the ATH attributes an increase in residence with age to enhanced breeding territory acquisition and maintenance, survival differences between phenotypes may also play an important role (Acker, Daunt, et al., 2021; Snell et al., 2021). We found lower survival in residents than migrants in young females, albeit with high uncertainty, and higher survival in residents than migrants in adult males. These observations correspond well to the observed age-dependent patterns in transition probabilities. Increasing experience with age may also contribute to these patterns, as age is often correlated with improved foraging efficiency (Cunningham et al., 2017; Daunt et al., 2007). This could give older birds an advantage during

limited resource scenarios, such as in the breeding area during winter, consistent with an increasing probability of residence with age.

For adult males, in particular, migrants appeared to incur a substantial survival cost compared to residents, though this pattern was not evident in females. This result appears to contradict the assumption regarding survival in migrants and residents underlying both the ATH, as well as the BSH; namely, that residents are exposed to harsher environmental conditions over winter and, thus, experience a larger survival cost compared to migrants. In addition to these results, a recent meta-analysis by Buchan et al. (2020) suggested that, in vertebrates, residence increasingly confers survival benefits, likely as a result of anthropogenic environmental change, such as milder winters and food subsidies (Rotics et al., 2017). However, previous studies often found lower survival in juvenile, but not adult migrants (Buechley et al., 2021; Sanz-Aguilar et al., 2015; but see Lok et al., 2011; Morant et al., 2022). The difference found here between migrant and resident males is unlikely to be due to exposure to greater threats during the overwintering period because then we would expect a similar difference in survival between migrant and resident females. This is because, in our population, males and females use similar migratory routes and wintering areas. Instead, we speculate that the energetic cost to annually acquire or re-acquire a breeding territory may manifest itself in lower survival in migratory males (Grande et al., 2009; Ord, 2021; Sanz-Aguilar et al., 2017). Similarly, migrants may be forced to occupy territories with poorer food resources than residents, resulting in higher intrinsic costs of reproduction and lower survival (Grande et al., 2009; Michel et al., 2022). Ultimately, these results present a novel perspective on how partial migration is maintained in populations and when and how individuals transition from a migrant to resident lifestyle as they age. Furthermore, our results suggest that a reproductive advantage for residents may not be necessary to observe an increase in the occurrence of residence with age, nor an increase over time within a population.

4.2 | Body size hypothesis: Size matters in females

We found evidence for an effect of body size on transition probability in females, but not males. Other studies of partially migrant species have provided evidence of size playing a role in migratory phenotypic expression, mostly attributed to improved thermoregulation and fasting endurance (Boyle, 2008; Fudickar et al., 2013; Hegemann et al., 2015). However, age and sex-dependent differences in the effect of size, as found here, are still largely unrecognized even if age and sex-dependent effects of body mass have been shown previously (Jahn et al., 2010). This corroborates the importance of accounting for different factors simultaneously influencing migratory phenotype. We see two potential explanations for the body size pattern found here: (1) Females might have lower fasting endurance than males due to their role as egg-layers. Harsh environmental conditions on the breeding grounds demanding elevated energetic expenditure during winter (Morant et al., 2022) in

combination with a subsequent prezygotic contribution to egg production (Fudickar et al., 2013) could make residence more feasible for large than small breeding-aged females. (2) The high breeding density in our study area means that both males and females experience competition for breeding territories and/or mates (Kokko, Gunnarsson, et al., 2006). This competition might be size-dependent in females, but not males.

4.3 | Migration among adults

Despite the high residence transition probability within the adult age class, some adults continue to migrate. In addition to potential genetic effects (i.e. fixed phenotypes or high migratory liabilities; Pulido, 2011), we see multiple other non-mutually exclusive explanations for this pattern. Assuming that a main benefit of residence is territory acquisition and maintenance, consistent migrants may have simply been in the right place at the right time to claim a territory, or established territories during a period when population density was not as high. This assumes that migrants could reclaim those territories in subsequent years without becoming resident. A general lack of breeding dispersal in our study population (Scherler, van Bergen, et al., 2023) supports this assumption, suggesting that both migratory phenotypes benefit from an interannual prior residency effect (Forstmeier, 2002; Kokko, 2011; Kokko, López-Sepulcre, et al., 2006), giving the previous year's territory holder an advantage in territorial disputes. If this is the case, then the main reproductive benefit of residence may be territory acquisition at first reproduction rather than territory holding thereafter. Migrants may also enhance their territory acquisition ability by improving their pre-breeding body condition through overwintering in more hospitable areas than residents (Sirot & Touzalin, 2014). In addition, a periodic over-winter survival advantage for migrants resulting in temporally fluctuating selection may play a role in the maintenance of migration. In such a case, residents may experience a survival advantage or equal survival to migrants in "normal" winters, but a strong survival disadvantage in periodically occurring harsh winters (Acker, Burthe, et al., 2021; Acker, Daunt, et al., 2021). Depending on the frequency of harsh winters, this effect could be adequate to maintain the migrant phenotype in the adult population.

In addition to these ecological explanations, sample bias may contribute to variation in migration probability. An overrepresentation of younger adults among our adult age class, due to the relatively young age of the Swiss population resulting from the recent range expansion, may inflate the transition probability in our adult age class. Our inability to distinguish between younger versus older adults prevented us from detecting this potential age variation.

5 | CONCLUSIONS

Our results suggest that the factors underlying condition-dependent partial migration may operate in interaction, resulting

in complex within-population patterns of migratory phenotypes. A largely directional switch from migration to residence with increasing age is consistent with the ATH. Variation in the age at which individuals transition to residence suggests that other variables additionally modulate the probability of transitioning and may help explain why the migrant phenotype persists in adults. For example, body size appears to modulate the ontogeny of the residence transition in females, indicating an interactive contribution of factors underlying the BSH to those underlying the ATH. Increasing incidence of the residence transition around the age of first reproduction suggests that residence may maximize chances of territory establishment or offset increased survival costs of reproduction in males. Thus, increasing competition for breeding territories likely increases the fitness benefit of residence (Kikuchi & Reinhold, 2021; Kokko, 1999; Sirot & Touzalin, 2014), suggesting that population structure may play a role in determining migratory behaviour. Further studies are required to empirically investigate the relationships between migratory phenotype, recruitment, and population density. Ontogenetic patterns in survival corresponded well with those in transition probability, indicating that selection also plays an important role in migratory phenotypic expression across ontogeny. Ultimately, understanding how condition-dependent mechanisms affect the migratory phenotype requires the joint assessment of multiple underlying factors acting simultaneously during ontogeny, particularly around the age of first reproduction.

AUTHOR CONTRIBUTIONS

Stephanie Witczak, Martin U. Grüebler and Urs Kormann conceived the study. Stephanie Witczak collected and analysed the data with critical conceptual and analytical help from Michael Schaub and Steffen Oppel. Stephanie Witczak drafted the manuscript with critical input from Martin U. Grüebler, Urs Kormann, Michael Schaub and Steffen Oppel. All authors contributed to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo Open Digital Repository: <https://doi.org/10.5281/zenodo.10479283> (Witczak et al., 2024).

STATEMENT OF INCLUSION

Our study brings together authors from multiple countries, including scientists from the country where the study was carried out. Local scientists and stakeholders were engaged early on with the research and study design.

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SUPPORTING INFORMATION

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

Supporting Information S1. Additional methods and results.

Supporting Information S1.1. Body size population distribution.

Supporting Information S1.2. Migratory phenotype determination.

Supporting Information S1.3. Description of the preparation and analysis of the tracking data.

Supporting Information S1.4. Proportion of residents across age (1–20CY).

Supporting Information S1.5. Detailed sample size.

Supporting Information S1.6. Detailed model output.

Supporting Information S2. Code.

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