



# Female-biased dispersal and non-random gene flow of *MC1R* variants do not result in a migration load in barn owls

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## Abstract

Non-random gene flow is a widely neglected force in evolution and ecology. This genotype-dependent dispersal is difficult to assess, yet can impact the genetic variation of natural populations and their fitness. In this work, we demonstrate a high immigration rate of barn owls (*Tyto alba*) inside a Swiss population surveyed during 15 years. Using ten microsatellite loci as an indirect method to characterize dispersal, two-third of the genetic tests failed to detect a female-biased dispersal, and Monte Carlo simulations confirmed a low statistical power to detect sex-biased dispersal in case of high dispersal rate of both sexes. The capture–recapture data revealed a female-biased dispersal associated with an excess of heterozygote for the melanocortin-1 receptor gene (*MC1R*), which is responsible for their ventral rufous coloration. Thus, female homozygotes for the *MC1R*<sub>WHITE</sub> allele might be negatively selected during dispersal. Despite the higher immigration of females that are heterozygote at *MC1R*, non-random gene flow should not lead to a migration load regarding this gene because we did not detect an effect of *MC1R* on survival and reproductive success in our local population. The present study highlights the usefulness of using multiple methods to correctly decrypt dispersal and gene flow. Moreover, despite theoretical expectations, we show that non-random dispersal of particular genotypes does not necessarily lead to migration load in recipient populations.

## Introduction

Unraveling the effect of natural selection and dispersal in shaping genetic and phenotypic variation is crucial to understand the impact of gene flow on local adaptation. Dispersal can counteract the effect of natural selection by introducing maladapted alleles into locally adapted populations (Slatkin 1987; Hu and Li 2003), an effect that depends on the strength of selection against immigrants and the alleles they carry (Lenormand 2002; Postma and van Noordwijk 2005). This is referred to as “migration load,”

when the fitness of a population decreases as a result of the immigration of locally less fit alleles (Garcia-Ramos and Kirkpatrick 1997; Bolnick and Nosil 2007). However, the absence of dispersal, and consequently gene flow, can limit local adaptation due to decreased genetic variation on which natural selection can work (Bourne et al. 2014). Dispersal can indeed potentially facilitate the exchange of adaptive variation between populations (Bolnick and Otto 2013; PortnFulgioneoy et al. 2015; Fulgione et al. 2016) or even among closely related species that hybridize (Fraisie et al. 2014; Palmer and Kronforst 2015).

Gene flow plays a major role in evolutionary processes, but its effects are generally complex (Ciani and Capiluppi 2011; Edelaar and Bolnick 2012; Bolnick and Otto 2013). Dispersal is often not a set of random individuals moving between populations, but instead can be enriched for certain phenotypes and underlying genotypes, as shown in humans for the *DRD4* gene, which is associated with novelty seeking and hyperactivity traits (Chen et al. 1999). Dispersal is also often sex biased in vertebrates [e.g., female biased in common frogs *Rana temporaria* (Palo et al. 2004) or in cougars *Puma concolor* (Biek et al. 2006); male biased in white-throated magpie-jays *Calocitta formosa* (Berg

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et al. 2009) or in tortoises *Astrochelys radiata* (Paquette et al. 2010)] meaning that dispersal and gene flow could differentially impact male and female fitness (Tarka et al. 2014; Camacho et al. 2013). Thus, describing gene flow based on particular genotypes or gender is important to understand how dispersal could favor or constrain the adaptive effects of natural selection within populations in a sex-specific manner (Edelaar and Bolnick 2012).

In natural populations, dispersal and gene flow can be estimated with direct methods that measure the movement of individuals through capture–recapture (Conrad et al. 1999; Baguette 2003; Schtickzelle et al. 2006) or GPS-tracking methods (Cooke et al. 2004; Ropert-Coudert and Wilson 2005). However, the direct assessment of dispersal can be difficult or inaccurate, such as in smaller-sized organisms, which preclude direct marking, or in large populations, where a relatively small proportion of animals can be marked, which impede detection of dispersers. Indirect methods based on genetic data offer an alternative approach to estimate dispersal and gene flow by comparing genotype frequencies between populations (Wright 1943; Wright 1951; Slatkin 1985) or between sexes (Goudet et al. 2002; Hansson et al. 2003). In many instances indirect methods are inaccurate in estimating gene flow or population divergence, for example, when individual movements are asymmetric between populations (Boileau et al. 1992; Knutsen et al. 2011). This is why the combination of direct and indirect approaches is useful to underline the importance of dispersal and gene flow in shaping neutral genetic variation (Slatkin 1985), as shown in damselfly *Coenagrion mercuriale* (Watts et al. 2007), Atlantic cod *Gadus morhua* (Knutsen et al. 2011), alpine salamander *Salamandra atra* (Helfer et al. 2012), and social weavers *Philetairus socius* (van Dijk et al. 2015), or in shaping phenotypic and neutral genetic variation in blue tits *Cyanistes caeruleus* (Garcia-Navas et al. 2014). However, further empirical studies that combine both methodologies to clarify the effect of dispersal and gene flow in shaping adaptive genetic variation are required because most studies performed so far considered only neutral genetic markers.

The European barn owl (*Tyto alba*) is an appropriate model system to study the effect of dispersal on neutral and adaptive genetic variation. The striking variation of its pheomelanin-based coloration is associated with a non-synonymous mutation at the melanocortin-1 receptor gene (*MC1R*) (San-Jose et al. 2015; Burri et al. 2016), a key element in the vertebrate melanin synthesis pathway (Bennett and Lamoreux 2003). The valine allele (hereafter referred to as V, white, allele) is strongly related with a white ventral plumage coloration, whereas the isoleucine (hereafter referred to as I, rufous, allele) relates to a redder plumage coloration and seems always partially dominant over the white allele. The pheomelanin coloration and its

underlying *MC1R* alleles vary clinally in Europe, from high frequency of the *MC1R*<sub>WHITE</sub> allele in the Iberian Peninsula to a high frequency of the *MC1R*<sub>RUFIOUS</sub> allele in northeast Europe, while both mutations occur at intermediate frequencies in Central Europe (Antoniazza et al. 2010; Burri et al. 2016). At neutral markers, a significant albeit weak differentiation between European populations ( $F_{st} = 0.011$ ; 99% CI: 0.007–0.016, see Antoniazza et al. 2010) highlights high gene flow at the level of the continent. Therefore, the maintenance of both genetic and phenotypic clines, despite strong gene flow, supports the presence of local adaptation (Antoniazza et al. 2010), as demonstrated through ABC simulations (Antoniazza et al. 2014). On a smaller spatial scale, there is also evidence for local adaptation in Switzerland, where coloration of females matches specific habitat types (Dreiss et al. 2012) and coloration is related to different prey–predator strategies (Roulin 2004; Charter et al. 2012). Moreover, the *MC1R*<sub>RUFIOUS</sub> mutation seems to be recurrently counter-selected in males at the juvenile stage (Ducret et al. 2016).

Here, we explore the effect of dispersal on the frequency of *MC1R* variants in breeding barn owls of a Swiss population. First, we investigated if *MC1R* genotypes deviate from Hardy–Weinberg equilibrium and if the deviation is different in male and female breeders, which could be caused by the effect of sex-specific selection and/or sex-biased dispersal. To disentangle which of these two processes is the most likely cause of a deviation, we also analyzed Hardy–Weinberg at ten neutral genetic markers (microsatellite loci). Because the Swiss barn owl population is at an intermediate position along the European cline, we would expect gene flow to cause a deficit rather than excess of heterozygotes for both microsatellites and *MC1R*. This is due to the genetic admixture of differentiated populations (containing a high proportion of homozygous individuals) from each extremity of the cline, also known as the Wahlund effect (Wahlund 1928). We analyzed capture–recapture data and neutral genetic data, respectively, direct and indirect methods, to characterize and estimate immigration rate of the *MC1R* genotypes and to test if dispersal is female biased, as generally found in birds (Trochet et al. 2016). Lastly, we tested for sex-specific selection on *MC1R* genotypes in adults by analyzing reproductive success and survival.

## Materials and methods

### Data collection

The study was performed from 1998 to 2016 in an area of 1070 km<sup>2</sup> in western Switzerland, where wild breeding barn owls were captured in artificial nest boxes. During the study

period, we captured between 22 and 125 (mean = 57) breeding pairs annually. Clutch size and number of fledglings (i.e., viable offspring up to the fledging stage) were recorded for each nest, and all nestlings and 90% of breeding adults were captured and marked with aluminum rings since 1988. Ringing allowed us to differentiate adults born inside our study area (philopatric) from those born outside (immigrant). Immigrants were those ringed outside the area by amateur ornithologists or captured for the first time without a ring. Immigrants' age can be estimated based on the molting pattern of the primary wing feathers (Dreiss and Roulin 2010).

We collected and stored blood samples of all captured barn owls at  $-80^{\circ}\text{C}$  until DNA extraction. DNA was extracted using the DNeasy Tissue and Blood kit or the Biosprint robot (Qiagen). We determined *MC1R* genotypes for all adults by allelic discrimination (see protocol in San-Jose et al. 2015). The allelic discrimination (AD) assay is a methodology using fluorescent markers of mutant and wild-type probes that provides a rapid and sensitive method for detecting known polymorphisms. Each probe consists of an oligonucleotide with a 5' reporter dye and a 3' quencher dye. In our case, the fluorescent markers of mutant and wild-type probes are ATTO550 and FAM, respectively (Microsynth). Therefore, if at the end of the qPCR there is fluorescence from only the reporter (FAM) for the wild-type allele, the sample is typed as VV. Fluorescence from only the ATTO550 reporter represents homozygosity for the mutant allele and is genotyped as II. Intermediate fluorescence from both reporters represents heterozygotes (VI). In each assay, we ran positive controls for each genotype and each sample was run in duplicate with two different PCRs. Only adults from 1998 to 2012 ( $N = 755$ ) were genotyped for ten polymorphic microsatellite loci in two sets of multiplex. Genotyping procedure and description of multiplex sets (named 3 and 4) are described by Burri et al. (2016). Thus, the genetic analyses were constrained to the period 1998–2012, comprising the samples of 316 males and 439 females. They were used to estimate sex-biased dispersal and Hardy–Weinberg proportions at both *MC1R* and microsatellites and for assignment tests.

## Genetic analyses

### MC1R proportions

Deviation from Hardy–Weinberg equilibrium ( $F_{IS}$ ) at *MC1R* was computed for each year using FSTAT v2.9.3 (Goudet 1995) and the difference between males and females on the range of  $F_{IS}$  values was tested using Wilcoxon signed-rank test. We tested for differences in the proportion of *MC1R* genotypes between immigrant and philopatric males and females using a Fisher's exact test and

computed the  $F_{IS}$  values per sex and dispersal status (i.e., resident vs. immigrant) with FSTAT.

### Sex-biased dispersal

The difference in the proportion of immigrants between the two sexes was assessed by means of a  $\chi^2$ -test using capture–recapture data. In addition, we used microsatellite data to detect female-biased dispersal by quantifying the mean assignment index ( $mAI_c$ ) and variance of the assignment index ( $vAI_c$ ) separately for both sexes using the R package HIERFSTAT (Goudet 2005; R Core Team 2013) and significant differences were determined using a one-tailed permutation test ( $N = 1000$ ). Deviations from Hardy–Weinberg equilibrium ( $F_{IS}$ ) per year of sampling were also computed using FSTAT and differences between males and females on the range of  $F_{IS}$  values were tested using the Wilcoxon signed-rank test. Sex-biased dispersal is expected to result in a lower  $mAI_c$  and larger  $vAI_c$  in the dispersing sex as well as positive  $F_{IS}$  values due to a stronger Wahlund effect among adults of the dispersing sex (see Goudet et al. 2002).

### Individual-based Monte Carlo simulations

The large percentage of immigrants (71%), calculated from the capture–recapture data of adults, compared to residents in our study area and the fact that the tests were performed on a single population may decrease the sensibility of the  $mAI_c$  and  $vAI_c$  tests in detecting sex-biased dispersal. Therefore, we estimated the statistical power of  $mAI_c$  and  $vAI_c$  using individual-based Monte Carlo simulation from EASYPOP (Balloux 2001), with the dispersal rate of males and females estimated by capture–recapture (respectively,  $d_m = 0.62$  and  $d_f = 0.78$ ) and with ten simulated loci. Dispersal followed an island model, the chosen mutation rate was 0.001 with 25 allelic states and the KAM mutation model (see detailed description of the parameters by Goudet et al. 2002). The simulation ran with ten populations containing each 50 males and 50 females, which represent the average annual number of breeding males and females in our study area. To achieve mutation–migration–drift equilibrium, each of 99 replicates was run for 1000 generations. We also simulated a higher sex-biased dispersal, once with a total dispersal rate similar to the previous simulation ( $d_m = 0.5$  and  $d_f = 1.0$ ,  $d_t = 0.75$ ), and then with a lower total dispersal rate ( $d_m = 0$  and  $d_f = 0.5$ ,  $d_t = 0.25$ ). Finally, we applied the  $mAI_c$  and  $vAI_c$  tests using HIERFSTAT to a single or all-simulated populations and for each replicate. Thus, we defined the statistical power of the two tests in detecting female-biased dispersal as the number of times the tests were significant ( $P \leq 0.05$ ) over the 99 replicates.

## Fitness components

To estimate fitness, we measured survival and reproductive success of the *MC1R* genotypes. Because homozygotes for the *MC1R*<sub>RUF</sub> were rare (~3%), we distinguished genotypes as carrying at least one vs. no copy of the *MC1R*<sub>RUF</sub> allele (i.e., II/VI vs. VV).

### Survival probability

Annual capture–recapture data of adult barn owls that have been collected in our study area from 1998 to 2016 were analyzed with Cormack–Jolly–Seber (CJS) models (Lebreton et al. 1992) using the program MARK (White and Burnham 1999). Nine hundred ninety-six captured adults were sexed, genotyped at *MC1R* (II/VI vs. VV), with known dispersal status (either locally born or immigrant) and thus constituted eight groups of individuals. We estimated apparent survival ( $\varphi$ ), which is the probability to survive and to remain in the study area. Although we cannot distinguish between mortality and emigration, both processes lead to similar effects on the fitness of individuals at the local population level. We estimated the recapture probabilities ( $\rho$ ), which is the probability to recapture a marked individual present in the study area. We started with a general model that assumed survival to vary over time in each of the eight groups independently from each other and for which the recapture probability varied over time in males and females independently from each other. In the first modeling step, we verified whether survival and recapture probabilities varied over time and whether temporal variation was additive to the group effects. In the second modeling step, we kept the recapture model at the most parsimonious structure and modeled the effects of the eight groups on survival. Specifically, we fitted all possible models including single effects of sex, dispersal status, *MC1R* genotype, and their two-way and three-way interactions. At each step, we fitted several candidate models that were ranked based on Akaike Information Criterion corrected for small sample sizes (AIC<sub>c</sub>; Burnham et al. 2011). We verified the goodness-of-fit of the most complex model with the program U-CARE (Choquet et al. 2009). This test showed a good fit ( $\chi^2 = 102.08$ ,  $df = 159$ ,  $P = 0.99$ ).

### Reproductive success

We analyzed components of reproductive success in each nest from 1998 to 2016 with respect to sex, dispersal status (immigrant vs. resident), and *MC1R* genotypes (II/VI vs. VV) using generalized linear mixed models (GLMMs with single effects and their two-way and three-way interactions). Clutch size and the number of fledglings produced

were analyzed using Poisson errors, whereas fledging success (probability that an egg become a fledgling) was analyzed using binomial errors. In all models, the laying date was incorporated as covariate and standardized (scaled and centered) to ease model convergence. Adults' and sites' identities and year were incorporated as random factors to account for spatial and temporal pseudo-replication. Competing models were ranked based on the AIC<sub>c</sub> using the function “dredge” of package MuMIn (Barton 2016) and the model with the lowest AIC<sub>c</sub> score was selected as the best-fitting model. Overdispersion was checked for all models using the function “overdisp.glmer” of the package RVAideMemoire (Hervé 2016). The statistical analyses were conducted with the R software v3.2.4 (R Core Team 2013).

## Results

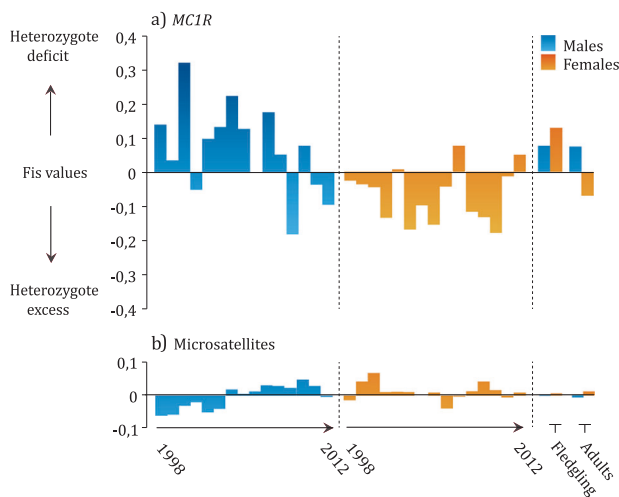
### Hardy–Weinberg proportion at microsatellites and *MC1R*

A total of 105 alleles were found across the ten microsatellite loci. The number of alleles per locus ranged from 4 (locus Ta202) to 25 (locus Ta402). Randomization of alleles within sampling years indicated that in males one marker presented significant positive  $F_{IS}$  (0.154) and two markers significant negative  $F_{IS}$  (−0.061 and −0.1) after Bonferroni correction ( $P < 0.001$ ; Table 1). In females, one marker (Ta212) presented significant positive  $F_{IS}$  (0.062) after Bonferroni correction ( $P < 0.001$ ; Table 1). We discovered

**Table 1**  $F_{IS}$  values in adult male and female barn owls for ten microsatellite loci averaged over 1998–2012

	Males		Females	
	$F_{IS}$	$P$ values	$F_{IS}$	$P$ values
Ta202	0.154	<b>&lt;0.001</b>	0.037	0.108
Ta204	0.010	0.340	0.008	0.362
Ta212	−0.030	0.058	0.062	<b>&lt;0.001</b>
Ta214	0.016	0.253	0.029	0.087
Ta215	−0.025	0.181	0.046	0.049
Ta305	−0.023	0.169	0.047	0.033
Ta310	−0.100	<b>&lt;0.001</b>	0.036	0.068
Ta402	−0.012	0.153	−0.028	0.009
Ta408	0.009	0.338	−0.051	0.003
Ta413	−0.061	<b>&lt;0.001</b>	−0.003	0.392

$P$  values correspond to the proportion of randomizations that gave a larger or a smaller  $F_{IS}$  than the observed value (respectively, when  $F_{IS}$  is positive or negative). Bold  $P$  values indicate significant deviation from HW proportion under a risk  $\alpha = 0.05$  and after Bonferroni correction ( $P$  value is divided by 10 (number of loci tested) and by 2 (number of sex tested, i.e.,  $P < 0.0025$ )).



**Fig. 1**  $F_{IS}$  values computed for *MC1R* and microsatellites and averaged over loci per year of sampling and sex in breeding barn owls. Positive and negative values represent, respectively, deficit and excess of heterozygote at *MC1R* or microsatellites

the presence of null alleles for this marker and we removed it for all adults in the subsequent analyses. Also, females did not show significantly higher annual  $F_{IS}$  values (average  $F_{IS} = 0.011$ ,  $F_{IS}$  year-range =  $-0.039$  to  $0.067$ ) than males (average  $F_{IS} = -0.005$ ,  $F_{IS}$  year-range =  $-0.061$  to  $0.047$ ) (Wilcoxon sum rank test,  $W = 131$ ,  $P = 0.23$ ).

The pattern at *MC1R* was different compared to neutral markers. Adult females showed a significantly higher excess of heterozygotes (average  $F_{IS} = -0.069$ ,  $F_{IS}$  year-range =  $-0.18$  to  $0.076$ ) than males (average  $F_{IS} = 0.077$ ,  $F_{IS}$  year-range =  $-0.182$  to  $0.319$ ) (Wilcoxon rank sum test,  $W = 42.5$ ,  $P = 0.004$ ; Fig. 1).

## Dispersal and gene flow

Our capture–recapture data indicated that only 29% of the adults breeding in our study area were born inside the study area. The proportion of locally born breeders was higher in males compared to females (38% vs. 22%; Chi-square test,  $\chi^2 = 24.26$ ,  $P < 0.001$ ; Table 2). Using microsatellite data, we observed a weak but significantly higher variance assignment index for females than for males (respectively  $vAI_{cf} = 11.03$ ,  $vAI_{cm} = 9$ ; permutation test,  $P = 0.021$ ), but the mean assignment index ( $mAI_c$ ) was close to 0 in both sexes ( $P = 0.48$ ).

In females, immigrants were more often heterozygous for the *MC1R* gene than residents (Fisher's exact test,  $P = 0.042$ ), while in males we did not find such a difference ( $P = 0.93$ ; Table 2). Those differences in the level of heterozygosity between immigrants and residents within each sex were reflected in the  $F_{IS}$  values, although the deviations were not significant. Philopatric females showed an excess of homozygotes ( $F_{IS} = 0.197$ ,  $P = 0.05$ ) and immigrant

**Table 2** Numbers and percentages of *MC1R* genotypes in philopatric and immigrant male and female barn owls breeding in western Switzerland between 1998 and 2012

	II	VI	VV	Total
<i>Males</i>				
Philopatric	4 (3.3%)	31 (25.4%)	87 (71.3%)	122
Immigrant	7 (3.6%)	54 (27.8%)	133 (68.6%)	194
<i>Females</i>				
Philopatric	5 (5.2%)	21 (21.9%)	70 (72.9%)	96
Immigrant	5 (1.5%)	101 (29.4%)	237 (69.1%)	343

II: homozygotes for the *rufous* allele, VI: heterozygotes, VV: homozygotes for the white allele

females a slight excess of heterozygotes ( $F_{IS} = -0.084$ ,  $P = 0.1$ ), whereas we observed a slight excess, albeit non-significant, of homozygotes in both philopatric ( $F_{IS} = 0.058$ ,  $P = 0.33$ ) and immigrant males ( $F_{IS} = 0.040$ ,  $P = 0.35$ ).

## Statistical power of $vAI_c$ and $mAI_c$ tests

The  $mAI_c$  and  $vAI_c$  tests have a very low power to detect female-biased dispersal when the dispersal rate is as high as observed in our study population ( $d_m = 0.62$  and  $d_f = 0.78$ ). Only 2% and 6% of the replicates had a significant  $vAI_c$  and  $mAI_c$  test, respectively. The statistical power did not increase when, for a similar mean dispersal rate, the sex-biased dispersal increased ( $d_m = 0.5$  and  $d_f = 1.0$ ) with 6% and 7% of the replicates having significant  $vAI_c$  and  $mAI_c$  tests, respectively. The power of the  $mAI_c$  and  $vAI_c$  tests did not differ and was always very low when the tests were performed on a single or on all-simulated populations.

With a reduced average dispersal rate (0.25) but with the same strong sex-biased dispersal as previously ( $d_m = 0.0$  and  $d_f = 0.5$ ), the power of the two tests increased drastically with 50% and 92% of the replicates having significant  $vAI_c$  and  $mAI_c$  tests, respectively, and when the tests were performed on the data containing the ten populations. If the tests were performed on a single population, the  $vAI_c$  test became significant in only 9% of the cases, whereas the  $mAI_c$  test was significant in 30% of the cases. The lower statistical power of the  $vAI_c$  compared to the  $mAI_c$ , when the dispersal rate is low, was expected based on previous simulations (Goudet et al. 2002).

## Apparent survival in relation to *MC1R*

The model with time-specific recapture probabilities and time-dependent survival probabilities with an additive group effect was by far the most parsimonious model (Table S1). Although the model with an additive sex effect on recapture probability was close to the best

**Table 3** Model selection results of apparent survival ( $\varphi$ ) of adult barn owls breeding in western Switzerland in function of time ( $t$ : year), sex, dispersal status (status: immigrant vs. resident) and *MCIR* genotypes (*MCIR*: II/VI vs. VV)

Model	AIC <sub>c</sub> <sup>a</sup>	$\Delta$ AIC <sub>c</sub> <sup>b</sup>	w <sup>c</sup>	K	Deviance
$\varphi(\text{Sex} + \text{status} + t)$	2191.23	0.00	0.34	37	785.17
$\varphi(\text{Sex} + \text{status} + \text{MCIR} + t)$	2192.63	1.40	0.17	38	784.46
$\varphi(\text{Sex} + \text{status} + \text{sex} * \text{status} + t)$	2193.34	2.11	0.12	38	785.17
$\varphi(\text{Sex} + \text{status} + \text{MCIR} + \text{sex} * \text{MCIR} + t)$	2193.80	2.57	0.09	39	783.51
$\varphi(\text{Sex} + \text{status} + \text{MCIR} + \text{MCIR} * \text{status} + t)$	2194.27	3.04	0.07	39	783.98
$\varphi(\text{Sex} + \text{status} + \text{MCIR} + \text{sex} * \text{status} + t)$	2194.74	3.51	0.06	39	784.46
$\varphi(\text{Sex} + \text{status} + \text{MCIR} + \text{sex} * \text{MCIR} + \text{MCIR} * \text{status} + t)$	2195.14	3.91	0.05	40	782.73
$\varphi(\text{Sex} + \text{status} + \text{MCIR} + \text{MCIR} * \text{status} + \text{sex} * \text{status} + t)$	2195.14	3.91	0.05	40	782.73
$\varphi(\text{Sex} + \text{status} + \text{MCIR} + \text{sex} * \text{MCIR} + \text{sex} * \text{status} + t)$	2195.92	4.69	0.03	40	783.51
$\varphi(\text{Sex} + \text{status} + \text{MCIR} + \text{sex} * \text{MCIR} + \text{sex} * \text{status} + \text{status} * \text{MCIR} + \text{sex} * \text{status} * \text{MCIR} + t)$	2199.05	7.83	0.01	42	782.41
$\varphi(\text{Sex} + t)$	2199.40	8.17	0.01	36	795.45
$\varphi(\text{Sex} + \text{MCIR} + t)$	2200.56	9.33	0.00	37	794.50
$\varphi(\text{Sex} + \text{MCIR} + \text{sex} * \text{MCIR} + t)$	2201.60	10.37	0.00	38	793.43
$\varphi(\text{Status} + t)$	2205.87	14.64	0.00	36	801.91
$\varphi(\text{MCIR} + \text{status} + t)$	2207.69	16.46	0.00	37	801.62
$\varphi(\text{MCIR} + \text{status} + \text{MCIR} * \text{status} + t)$	2209.22	17.99	0.00	38	801.05
$\varphi(\text{MCIR} + t)$	2225.46	34.23	0.00	36	821.51

Note that the model for recapture probability ( $\rho$ ) was always time dependent ( $t$ ) and is not included in the model notation. The most complex model for survival (i.e. (sex + status + *MCIR* + sex \* *MCIR* + sex \* status + status \* *MCIR* + sex \* status \* *MCIR* + t)) corresponds exactly to model ( $g + t$ ) from the first modeling step (see Table S1)

K: Number of parameter estimated

Deviance: model deviance

<sup>a</sup>AIC value corrected for small sample sizes

<sup>b</sup>Difference in a model's AIC<sub>c</sub> to the best-ranked model's AIC<sub>c</sub>

<sup>c</sup>Model weight: probability of the model given the data

model, it did not improve the prediction of survival regarding sex, dispersal status, or *MCIR* (Table S2). The best model with time-dependent recapture and apparent survival probabilities included an additive effect of sex and dispersal status on apparent survival (Table 3). Females had lower apparent survival than males ( $\beta = -0.526$ , 95% CI =  $-0.763$  to  $-0.288$ ) and immigrants had lower apparent survival than locally born individuals ( $\beta = -0.404$ , 95% CI =  $-0.652$  to  $-0.156$ ). An additive effect of *MCIR* was observed in the second-best model ( $\Delta$ AIC<sub>c</sub> = 1.40), where individuals with at least one copy of the *rufous* allele tended to have lower survival than homozygotes for the white allele ( $\beta = -0.110$ , 95% CI =  $-0.367$ – $-0.146$ ).

### Reproductive success in relation to *MCIR*

We did not find evidence that different *MCIR* genotypes produced different clutch sizes, number of fledglings, and clutch success (Table 4). Only in the third best model, we detected a tendency for an interaction between sex and

*MCIR* on the number of fledglings produced (GLMM Poisson,  $\chi^2 = 4.65$ ,  $P = 0.098$ ), while the single effect of *MCIR* was not significant ( $\chi^2 = 0.77$ ,  $P = 0.38$ ).

### Discussion

Disentangling the effect of selection and dispersal in natural populations is often challenging because both processes interplay in shaping genetic and phenotypic variation. Particularly, we barely understand the consequences of dispersal in shaping adaptive variation as most studies use neutral genetic variation to disentangle the effect of dispersal and selection (Mullen and Hoekstra 2008; Antoniazza et al. 2010). Here, in a barn owl population breeding in Switzerland, we explored the effect of dispersal on the local frequency of *MCIR* variants, a key two-alleles gene involved in vertebrate melanin synthesis pathway (Bennett and Lamoreux 2003) and suspected to be under local adaptation in Europe (Antoniazza et al. 2010, 2014).

**Table 4** Effects of *MC1R* genotypes (*MC1R*: II/VI vs. VV), sex, dispersal status (status: immigrant vs. resident) and laying date (LD) on components of reproductive parameters of adult barn owls

Predictors	AIC <sub>c</sub> <sup>a</sup>	ΔAIC <sub>c</sub> <sup>b</sup>	w <sup>c</sup>	K	Deviance
<i>Clutch size</i>					
LD	8074.2	0.00	0.45	5	8064.1
LD + status	8074.9	0.74	0.31	6	8062.9
LD + <i>MC1R</i>	8075.4	1.27	0.24	6	8063.4
<i>Number of fledglings produced</i>					
LD	8830.0	0.00	0.31	5	8820.0
LD + status + sex * status	8830.8	0.75	0.22	8	8814.7
LD + <i>MC1R</i> + sex * <i>MC1R</i>	8830.8	0.77	0.21	8	8814.7
LD + <i>MC1R</i>	8831.6	1.60	0.14	6	8819.6
LD + status	8831.9	1.92	0.1	6	8819.9
<i>Clutch success</i>					
LD	7926.1	0.00	0.35	5	7916.1
LD + status	7926.5	0.41	0.29	6	7914.5
LD + <i>MC1R</i>	7927.2	1.10	0.20	6	7915.2
LD + status + <i>MC1R</i>	7927.7	1.61	0.16	7	7913.6

Shown are the best models based on AIC<sub>c</sub> (ΔAIC<sub>c</sub> ≤ 2)

K: Number of parameter estimated

Deviance: model deviance

<sup>a</sup>AIC value corrected for small sample sizes

<sup>b</sup>Difference in a model's AIC<sub>c</sub> to the best-ranked model's AIC<sub>c</sub>

<sup>c</sup>Model weight: probability of the model given the data

### Comparison between direct and indirect estimates of sex-biased dispersal

Direct and indirect methods to estimate sex-biased dispersal have different strengths and weaknesses, and hence are complementary. Direct methods are often difficult to apply in natural populations but indirect methods based on neutral markers are sometimes not powerful enough to detect effects. Our results from capture–recapture analyses based on long-term monitoring of a Swiss barn owl population highlighted an overall high dispersal rate (71% of immigrants among breeding adults), which is in line with the low genetic differentiation at the scale of continental Europe due to intense gene flow (Antoniazza et al. 2010) and which seems to be common in other bird species as well (Schaub et al. 2013; Altwegg et al. 2014; Schaub et al. 2015). We also revealed that dispersal is female biased in barn owls, with 78% of females and 62% of males being immigrants.

The rate of immigration is so high in both sexes that the genetic (indirect) methods mostly failed to detect sex-biased dispersal with only the vAIC tests being significant. Accordingly, using simulations, we find an extremely low power of the mAIC and vAIC tests to detect the observed female-biased dispersal, which is due to the very high

dispersal rate in the Swiss population and the consideration of a single population (statistical power of the tests is higher if we compare dispersal between multiple populations). Because the assignment index tests are commonly performed on a single population or on small spatial scales (Chambers and Garant 2010; Liebgold et al. 2013; Harrison et al. 2014), we advise researchers to use several methods to estimate sex-biased dispersal in order to decrease the risk of type I and II errors. If dispersal rates are very large, indirect methods based on genetic markers will fail, because these methods assume the genotypes to represent a (imperfect) tag of the population where the individuals originated. In this situation, direct methods will probably generally be more powerful.

### Evolution of male-biased philopatry

The most acknowledged hypothesis to explain the evolution of sex-biased dispersal is in Greenwood's seminal paper Greenwood (1980), which linked the directionality of sex-biased dispersal to mating systems in birds and mammals. Using a database of 257 species and phylogenetic approaches, a recent review by Trochet et al. (2016) proposed that the evolution of sex-biased dispersal was linked to parental care and sexual dimorphism rather than to mating system per se, a pattern congruent to other findings in birds (Mabry et al. 2013). Among raptors and owls, sex roles in reproduction are well defined with females incubating, brooding, and distributing the food among the progeny and males hunting most of the prey items (Sonerud et al. 2014). Thus, the survival of the brood relies strongly on the hunting efficiency of males. Familiarity with the environment to acquire resources and potentially to attract females should therefore restrict male's dispersal and favor their philopatry (Ortego et al. 2008; Pakanen et al. 2016).

Concordant with this hypothesis, our results show that locally born individuals had higher apparent survival than immigrants, particularly in males. Locally born individuals also tended to produce slightly more fledglings than immigrants. Although our survival analyses could not distinguish between mortality and permanent emigration, it conclusively indicates that locally born males have a higher probability to reproduce inside our study area compared to females and immigrants. Importantly, a previous study on the population dynamics of this barn owl population showed that emigration from our study area is almost inexistent in adults (emigration rate: 0.010, SE = 0.014; Altwegg et al. 2003) because emigration in Swiss barn owls occurs mainly in yearlings (van den Brink et al. 2012), suggesting that our estimate of apparent survival in adults is close to true survival and hardly affected by emigration.

## Non-random dispersal

Dispersal is often related to morphological, behavioral, and ecological traits, also known as dispersal syndromes (Cote et al. 2010; Ronce and Clobert 2012; Chakarov et al. 2013). When dispersal is biased toward one sex, the dispersal traits may be differentially expressed between sexes. This covariation between sexual dimorphism and sex-biased dispersal arises from phenotype-related costs and benefits associated to dispersal (Tarka et al. 2014; Pakanen et al. 2016), as suggested for example with the evolutionary loss of female coloration with migration among wood-warblers (Simpson et al. 2015). In barn owls, previous studies found evidence that females move farther than males during natal and breeding dispersal, although individuals' pheomelanin coloration better explained variation in natal dispersal than sex (van den Brink et al. 2012; Roulin 2013). The relationship between dispersal and color could be easily explained by either a greater net costs of being visible while dispersing (i.e., being dark rufous is expected to be a cryptic coloration than a white phenotype), owing to risks of being detected by visual predators (Simpson et al. 2015) or to the fact that the melanocortin system is implicated in the expression of many phenotypic traits such as melanism, physiology, and behavior (Ducrest et al. 2008; Roulin and Ducrest 2011; Reissmann and Ludwig 2013).

Our results highlight that females—the dispersing sex—are more heterozygous than expected at *MCIR*, a gene with a valine-to-isoleucine substitution explaining ~30% of variation in the pheomelanin coloration in this population (San-Jose et al. 2015). Because homozygotes for the *MCIR<sub>RUF</sub>* allele are rare in the Swiss population and in nearby populations (Burri et al. 2016), the high frequency of heterozygotes results mostly from a deficit of homozygotes for the *MCIR<sub>WHITE</sub>* allele in immigrant females. However, based on our data set, we cannot test if this deficit is due to a cost for females to display a white phenotype or an advantage of being heterozygous at *MCIR* during dispersal. Future studies should compare individual's dispersal distance in populations where individuals are mainly white or dark rufous to further examine the effect of pheomelanin-based coloration on dispersal.

## Effect of sex-biased dispersal and non-random gene flow on fitness

Dispersal is often sex biased in vertebrates (Palo et al. 2004; Biek et al. 2006; Berg et al. 2009; Paquette et al. 2010; Trochet et al. 2016). As a matter of fact, theoretical and empirical studies have demonstrated that immigration of maladapted alleles results in a reduction of mean fitness of the recipient populations, also known as “migration load” (Garcia-Ramos and Kirkpatrick 1997; Bolnick and Nosil

2007). Moreover, if one sex has evolved to remain in their native site (philopatry), migration load will impact specifically this sex resulting in fitness differences between the philopatric and the dispersing sex (Tarka et al. 2014; Camacho et al. 2013). Thus, describing gene flow based on particular genotypes or gender is important to understand how dispersal favors or constrains the adaptive effects of natural selection within populations in a sex-specific manner (Edelaar and Bolnick 2012). Our analysis of apparent survival showed that immigrants have a lower survival than locally born individuals. Thus, while immigration may decrease the mean fitness of the population by introducing maladapted alleles, this effect should be reduced by the lower survival, and consequently reproduction, of immigrants compared to locally born individuals. In addition, we found in the second-best model of apparent survival that the *MCIR<sub>RUF</sub>* allele had only a weak and non-significant effect of decreasing apparent survival. Also, individuals carrying at least one copy of the *MCIR<sub>RUF</sub>* allele did not produce significantly fewer eggs or fledglings. Both results suggest that, despite the higher immigration of females that are heterozygote at *MCIR*, non-random gene flow should not lead to a migration load regarding this gene because *MCIR* has no effect on survival and reproductive success in our local population.

The presence of *MCIR* in the second-best survival model could suggest that selection is operating against the rufous coloration but the power to detect this effect is too low due to the fact that *MCIR* only explains a third of the variation in color. Future studies combining survival and reproductive success of differentially colored individuals into a general framework, using for example demographic models and elasticity approach, are needed to validate this hypothesis.

## Data archiving

Data (microsatellites and *MCIR* genotypes as well as the sex and year of capture of adult barn owls, the census data for the survival analysis, the fitness information) are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.584g6qg>.

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**Author contributions** AR and JG obtained funding; VD, AR, and JG conceived and designed the study; VD collected the *MCIR* and microsatellites data; AR conducted the field work; VD conducted the statistical and population genetic analyses; MS conducted the survival analysis; VD wrote the manuscript; and all the authors read and provided input on the manuscript.



## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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