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# Contrasting heterozygosity-fitness correlations across life in a long-lived seabird

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## Abstract

Selection is a central force underlying evolutionary change and can vary in strength and direction, for example across time and space. The fitness consequences of individual genetic diversity have often been investigated by testing for multilocus heterozygosity-fitness correlations (HFCs), but few studies have been able to assess HFCs across life stages and in both sexes. Here, we test for HFCs using a 26-year longitudinal individual-based data set from a large population of a long-lived seabird (the common tern, *Sterna hirundo*), where 7,974 chicks and breeders of known age were genotyped at 15 microsatellite loci and sampled for life-history traits over the complete life cycle. Heterozygosity was not correlated with fledging or post-fledging prospecting probabilities, but was positively correlated with recruitment probability. For breeders, annual survival was not correlated with heterozygosity, but annual fledgling production was negatively correlated with heterozygosity in males and highest in intermediately heterozygous females. The contrasting HFCs among life stages and sexes indicate differential selective processes and emphasize the importance of assessing fitness consequences of traits over complete life histories.

## KEYWORDS

common tern, fitness, heterozygosity, life history, microsatellites, *Sterna hirundo*

## 1 | INTRODUCTION

Selection is a central force underlying evolutionary change, and a dynamic process that can vary in strength and direction, for example across time and space (Endler, 1986). When males and females achieve reproductive success using different (behavioural and/or physiological) tactics, selection can also systematically differ between the sexes, leading to sexual conflict and/or sex-specific trait expression (Cox & Calsbeek, 2009). Moreover, selection can vary across life stages when (a) trait expression is affected by viability selection or ontogenetic processes (Hamel et al., 2016; Zhang, Vedder, Becker, & Bouwhuis, 2015a, 2015b), (b) early- and late-life performance are involved in a trade-off (Williams, 1957) and/or (c) there are age-specific causal agents of selection (Ditchkoff, Welch, Lochmiller, Masters, & Starry, 2001). Sex- and age-specific fitness

consequences of trait expression therefore are best studied in concert, across the entire lifespan and across multiple years if we are to understand the overall fitness effect of a trait.

Individual genetic diversity is one trait for which investigation of fitness consequences remains a central aim in evolutionary biology (Charlesworth & Charlesworth, 1999; Ellegren & Sheldon, 2008). For this purpose, individual genetic diversity is often measured as multilocus heterozygosity, then correlated to fitness proxies (heterozygosity-fitness correlations, HFCs; Chapman, Nakagawa, Coltman, Slate, & Sheldon, 2009; Coltman & Slate, 2003; Hansson & Westerberg, 2002; Miller & Coltman, 2014). Using markers that are presumed neutral (typically microsatellites), HFCs may arise through two mechanisms (Hansson & Westerberg, 2002). First, the measured heterozygosity may provide a good estimate of the genome-wide heterozygosity, which itself represents the individual

level of inbreeding and predicts fitness in cases of in- or outbreeding depression ("general effect hypothesis," Hansson & Westerberg, 2002). Second, HFCs may arise from linkage disequilibrium between a neutral marker and a functional locus if that functional locus is related to fitness ("local effect hypothesis," David, 1998). Although the capacity of microsatellite loci to reflect individual inbreeding has been questioned (Balloux, Amos, & Coulson, 2004; Nietlisbach et al., 2017; Townsend & Jamieson, 2013), quantification of the relative importance of local versus general effects is facilitated by using the appropriate statistical tools and workflow (David, Pujol, Viard, Castella, & Goudet, 2007; Stoffel et al., 2016; Szulkin, Bierne, & David, 2010).

Heterozygosity-fitness correlations have been extensively studied for over three decades (David, 1998; Szulkin et al., 2010) and reported across taxa (Chapman et al., 2009) and fitness proxies (e.g., survival: Kuepper et al., 2010; reproductive success: Velando, Barros, & Moran, 2015; competitive ability: Valimaki, Hinten, & Hanski, 2007; secondary sexual trait expression: Von Hardenberg et al., 2007; parasite resistance: Shaner, Chen, Lin, Kolbe, & Lin, 2013; immuno-competence: Fossey, Johnsen, & Lifjeld, 2009). The results, however, are equivocal, with reports of positive, negative and non-significant HFCs (Canal, Serrano, & Potti, 2014; Escobar, Nicot, & David, 2008; Grueber, Laws, Nakagawa, & Jamieson, 2010; Marshall & Spalton, 2000; Monceau, Wattier, Dechaume-Moncharmont, Dubreuil, & Cezilly, 2013; Neff, 2004; Olano-Marin, Mueller, & Kempenaers, 2011). HFCs which differ in sign both between and within studies may reflect quadratic associations between heterozygosity and overall fitness and thus an optimal level of heterozygosity for which fitness is maximal (Bateson, 1978; Bichet et al., 2014; Edmands, 2007; Ferrer, García-Navas, Sanz, & Ortego, 2014; Puurtinen, 2011). Moreover, inconsistency between HFCs could be explained by the fitness proxy used (Chapman et al., 2009; Coltman & Slate, 2003) or by variation in the environmental dependence of effects of heterozygosity on fitness (Armbruster & Reed, 2005; Szulkin et al., 2010) if studies do not span many years or a sufficiently large range of environmental conditions. Finally, HFCs could remain undetected when they are masked because unfavourable environmental conditions exert a stronger selection than heterozygosity (Annavi et al., 2014; Arct et al., 2017; Harrison et al., 2011), especially because HFCs are usually small (Chapman et al., 2009).

Sex-specific HFCs have often been reported (Arct et al., 2017; Shaner et al., 2013) and have been suggested to result from sex-specific parental investment (Charpentier et al., 2006) or differential life-history strategies in general (Ebel & Phillips, 2016; Shaner et al., 2013). For example, in the European shag (*Phalacrocorax aristotelis*), a positive correlation between heterozygosity, reproductive performance and survival was only detected in females (Velando et al., 2015). Conversely, a negative HFC with survival was observed in male, but not female, black-throated tits (*Aegithalos concinnus*) (Li, Wang, Lv, Wang, & Zhang, 2016). Studies comparing HFCs across life stages are rarer, but those that have been conducted have reported the direction and strength of HFCs to depend on the age of the individuals studied (Cohas, Bonenfant,

Kempenaers, & Allainé, 2009; Von Hardenberg et al., 2007; Keller, Reid, & Arcese, 2008; Monceau et al., 2013). In alpine marmots (*Marmota marmota*), for example, there was a positive correlation between heterozygosity and survival in juveniles, but not in yearlings, 2-years-olds or adults, which may be explained by the selective disappearance of low-heterozygous individuals (Cohas et al., 2009).

This diversity in findings suggests that studies of a single sex or life-history stage, or using only a single fitness proxy, could obscure our view by over-, under- or misestimating HFCs. Long-term studies across the lifespan of known-age individuals of both sexes are therefore crucial (Canal et al., 2014; Grueber et al., 2010; Von Hardenberg et al., 2007; Szulkin, Garant, McCleery, & Sheldon, 2007), and here, we investigate HFCs using 26 years of longitudinal individual-based data from a large population of a long-lived seabird, the common tern (*Sterna hirundo*). A total of 7,974 individuals were genotyped at 15 microsatellite loci to assess multilocus heterozygosity, a sample size which far exceeds the range (7–1,055) previously reported in a meta-analysis conducted by Chapman et al. (2009). For the 7,963 chicks included in this sample, we monitored the processes of fledging, local prospecting and local recruitment; for the 762 breeders, annual reproductive performance and survival. We evaluate HFCs across all life stages and assess the relative contribution of local versus general effects.

## 2 | MATERIAL AND METHODS

### 2.1 | Study population

Our data come from a long-term individual-based study of common terns from a mono-specific breeding colony located in a lake (the "Banter See") in Wilhelmshaven, on the German North Sea coast (53°36'N, 08°06'E). At this colony, chick ringing started in 1984, while large-scale individual-based monitoring started in 1992, when 101 breeders and all fledglings were individually marked with subcutaneous transponders (model ID 100; TROVAN, Germany; Becker & Wendeln, 1997). Since then, all local fledglings have been marked with such a transponder each year (Becker, Wendeln, & Gonzalez-Solis, 2001).

The colony site consists of six concrete islands (10.7 × 4.6 m each) surrounded by 60 cm high walls, which protect against flooding and prevent chicks from leaving their natal islands before fledging. The walls support 44 platforms for the terns to land on and rest. Each platform is equipped with an antenna which reads transponder codes at a distance of ≤11 cm every 5–10 s and therefore automatically records the presence of transponder-marked individuals. All transponder-marked breeders are additionally identified by placing an antenna around each clutch for at least 24 hr during incubation, which is shared between partners. Because birds have a high site fidelity and detection probability after recruiting, our long-term survey enables the systematic and remote documentation of individual life histories (Rebke, Coulson, Becker, & Vaupel, 2010; Zhang, Rebke, Becker, & Bouwhuis, 2015).

The sex of locally recruited breeders has been determined by standard molecular methods since 1998 (Becker & Wink, 2003) and was determined by behavioural observations after recruitment before that.

## 2.2 | Heterozygosity

Multilocus heterozygosity of 7,972 individuals was determined using 15 microsatellite markers (Janowski, Groß, Sauer-Gürth, Tietze, & Wink, 2016). Detailed information regarding the sampling, genotyping and microsatellite characteristics is presented in Supporting Information Appendix S1, but, in brief, DNA was obtained from feathers and tissue samples of 7,943 chicks and from blood of 29 adult breeders. For chicks ( $n = 7,943$ , see Supporting Information Table S1 in Appendix S1), DNA was obtained from body feathers plucked just prior to fledging ( $n = 3,605$ ) or from tissue samples collected from chicks found freshly dead ( $n = 4,338$ ). Moreover, 29 samples were collected from local breeders using a larval instar of the blood-sucking bug *Dipetalogaster maximus* (Heteroptera) placed in a hollow artificial egg temporarily added to the nests of focal birds during incubation. Eighteen of the 29 birds sampled as breeders were included in the chick data because their natal nest number, hatching order and number of siblings were known (see below). This way we obtained a total of 7,972 individual samples, comprising 7,961 locally hatched chick samples, covering the period 1998–2013, and 762 locally hatched breeder samples covering the period 1992–2016. The average number of loci genotyped per individual was  $14.21 (\pm 0.02 \text{ SE})$ .

Standardized observed heterozygosity ( $H_{s_{\text{obs}}}$ ) (Coltman, Pilkington, Smith, & Pemberton, 1999) was calculated using the R package GENHET (Coulon, 2010) and corresponds to the proportion of heterozygous loci (i.e., the number of heterozygous loci divided by the number of typed loci) divided by the average of the observed heterozygosity of all typed loci.

## 2.3 | Monitoring reproduction

Common terns are highly socially and genetically monogamous (Gonzalez-Solis, Sokolov, & Becker, 2001; Griggio, Matessi, & Marin, 2004) migratory seabirds that arrive at the colony site in early spring (Becker & Ludwigs, 2004). At the Banter See, 38% of fledglings are registered in later years as adults prospecting the colony and of those “prospectors” 65% eventually recruit to breed (Vedder & Bouwhuis, 2018). Once birds have established themselves as breeders, their annual survival and return rate are exceptionally high (90%; Ezard, Becker, & Coulson, 2006; Szostek & Becker, 2012). Since 1992, the number of breeding pairs ranged between 90 and 715.

Each breeding season, all nests are checked three times a week to record laying date, clutch size, brood size and fledging success. Newly hatched chicks are ringed at 0–2 days old and marked with transponders and weighed shortly before fledging. All chicks are thus reliably assigned to their parents, their nest of hatching and a hatching order (see also Vedder, Zhang, & Bouwhuis, 2017).

Clutch size varies between one and three eggs, which are laid and hatch with 1- to 2-day intervals (Becker & Ludwigs, 2004). Common terns rear one to three chicks per successful breeding attempt. While failed clutches may be replaced (Becker & Zhang, 2011; Wendeln, Becker, & Gonzalez-Solis, 2000), second clutches are extremely rare (Becker & Ludwigs, 2004; Moore & Morris, 2005).

## 2.4 | Life stages

### 2.4.1 | Hatching to fledging

Chick status (alive/dead) is recorded at each nest check. Most chicks that do not fledge are found dead, but missing chicks that are not yet at a stage ready to fledge are assumed to have died too. Chick disappearance results mostly from accidents caused by intraspecific aggression, with chicks ending up in the water and drowning, while other sources of “disappearance mortality,” such as predation, are rare (Becker, 2010). Chicks that survive to at least 18 days of age, and are not found dead later, are assumed to have fledged (Becker & Wink, 2003).

Between 1998 and 2013, 12,048 chicks (from 5,373 broods) hatched in our colony, of which 7,961 (66.1%) were genotyped (Supporting Information Appendix S1). Among these 7,961 chicks (from 3,934 broods), 3,623 fledged (45.5%), while 4,338 died (54.5%) (Supporting Information Appendix S1). Dead chicks were sampled regardless of their age of mortality. Among the 4,087 (33.9%) of the chicks that were excluded from our analyses, 954 fledged (23.3%) and 3,133 died (76.7%) (Supporting Information Appendix S1). This bias towards unsuccessful chicks among excluded chicks is caused by the fact that we, by definition, could not sample missing chicks. The causes of chick disappearance are, however, unlikely to be related to chick heterozygosity. 2,972 (55.3%) of the 5,373 broods had all their chicks genotyped, while 962 broods (17.9%) had at least one non-genotyped chick and 1,439 broods (26.8%) had no chicks genotyped (Supporting Information Appendix S1).

A chick's hatching order determines its competitive rank within a brood. Later-hatched chicks receive less food, grow more slowly, have a lower fledging mass (Becker & Wink, 2003), have a lower fledging probability and die at a younger age (Vedder et al., 2017) than their earlier-hatched siblings. In addition, fledging success is known to be affected by brood size, such that a first chick's fledging probability is higher in broods with one or two siblings than when it is alone (Vedder et al., 2017; Vedder, Zhang, Dänhardt, & Bouwhuis, in revision). To correct for these two aspects of a chick's natal environment, that affect fledging probability, but not later life stages (Vedder et al., in revision), we constructed a six-level categorical variable of all possible combinations of brood size and hatching order (1.1, 2.1, 2.2, 3.1, 3.2, 3.3), hereafter referred to as BSHO categories. Finally, because fledging success is known to be higher in broods produced earlier in the season (Dobson, Becker, Arnaud, Bouwhuis, & Charmantier, 2017), we used the Julian date of laying of the first egg of each clutch to describe a chick's natal environment as well.

**TABLE 1** Sample size, sampling period and average observed heterozygosity ( $H_{s_{obs}}$ ) across the different life stages of 7,972 common terns. Observed effects of  $H_{s_{obs}}$  are reported in the boxes

	Hatchlings	Fledglings	Prospectors	Breeders
Years	1998-2013	1998-2013	1998-2013	1992-2016
N individuals	7961	3607	1388	762 (426 males, 336 females)
N broods	3934	2578	1196	-
Average $H_{s_{obs}}$ ( $\pm$ SE)	0.9995 ( $\pm$ 0.002)	0.9991 ( $\pm$ 0.003)	0.9991 ( $\pm$ 0.005)	1.0071 ( $\pm$ 0.006) Males: 1.0052 ( $\pm$ 0.008) Females: 1.0095 ( $\pm$ 0.010)

Fledging probability was assessed as the status “fledged” or “dead” for 7,961 chicks of known heterozygosity, BSHO and laying date that hatched between 1998 and 2013 (Table 1).

#### 2.4.2 | Fledging to prospecting

Fledglings were considered successful prospectors when they returned to the colony within 5 years of fledging (independent of whether they bred or not). Each fledgling was attributed a 0 when it never returned after fledging or a 1 when it returned at least once. We assessed local prospecting for 3,607 fledglings of known sex and fledging mass between 1998 and 2013 (Table 1), using presence data up to 2018, such that all prospecting could be incorporated, since age at first prospecting averages 2.3 ( $\pm$ 1.0 SD) years (Vedder & Bouwhuis, 2018).

#### 2.4.3 | Prospecting to recruitment

Local recruitment probability was assessed using information on whether or not local prospectors ever bred at the colony. Each prospector was attributed a single value: we considered a prospector as not locally recruited if it was not detected as a breeder within 5 years of fledging, because 92% of adults first attempt reproduction within 5 years (Zhang, Rebke, et al., 2015) and age at recruitment averages 3.8 ( $\pm$ 1.3 SD) years (Vedder & Bouwhuis, 2018), in which case it was attributed a 0. Birds that bred within 5 years of fledging were attributed a 1. Using data up to 2018, we assessed recruitment for the 1,388 prospectors of known fledging mass, sex and age at first prospecting, which fledged between 1998 and 2013 (Table 1).

#### 2.4.4 | Breeding

Between 1992 and 2016, 762 local recruits (426 males, 336 females) of known age at first reproduction (AFR), age, sex and heterozygosity (Table 1) were observed in 3,353 bird-year combinations.

*Annual local survival* of these breeders was determined by checking whether an individual was registered by the antenna system during the breeding seasons between 1992 and 2018. Death was assumed if an individual was not registered for at least two consecutive years. The reliability of this assumption is high, since 97% of breeders do not skip observation for more than two consecutive years (Bouwuis, Vedder, & Becker, 2015; Zhang, Vedder, Becker, & Bouwhuis, 2015b).

*Annual local breeding probability* was assessed as whether or not a bird was observed incubating a clutch in a given year. A non-breeding status included years of observed skipped breeding (registered but not breeding,  $N = 183$  bird-years) as well as intermittent years of no observation ( $N = 88$  bird-years).

*Annual local reproductive success* was assessed as the total number of fledglings produced in a given year, regardless of whether these fledglings originated from first or replacement clutches. In total, the 762 recruited birds reproduced in 3,082 bird-years, of which the resulting number of fledglings was known for 3,079 breeding attempts.

#### 2.4.5 | Covariates

Survival of breeders was previously found to linearly decrease with age and to marginally differ between the sexes (Zhang, Rebke, et al.,

2015), which is why these variables were added to the annual local survival model. In addition, breeding probability is known to vary with age, while fledgling production varies with age and AFR (Rebke et al., 2010; Zhang, Rebke, et al., 2015; Zhang, Vedder, Becker, & Bouwhuis, 2015a), which were thus added as covariates to the models assessing reproductive performance. Following Zhang, Rebke, et al. (2015), AFR was categorized to occur at either age 2, 3, 4 or 5+. For our 762 local recruits, AFR averaged 3.49 ( $\pm 0.01$ ) years and was independent of  $H_{s_{obs}}$  ( $\beta = -0.004 \pm 0.02$ ,  $N = 761$ ,  $Z = -0.20$ ,  $p = 0.84$ ), confirming that both variables could be added to the model simultaneously.

Annual reproductive success is known to vary with arrival date (Dobson et al., 2017). Arrival date could, however, not be included as a covariate to the annual local reproductive success model, because it is strongly correlated with age in both sexes (males:  $t = -28.74$ ,  $df = 1,530$ ,  $R = -0.59$ ,  $p < 0.001$ ; females:  $t = -27.48$ ,  $df = 1,394$ ,  $R = -0.59$ ,  $p < 0.001$ ) (also see Zhang, Vedder, Becker, & Bouwhuis, 2015a). Arrival date was, however, not correlated with  $H_{s_{obs}}$  (males:  $\beta = -0.62 \pm 0.71$ ,  $N = 424$ ,  $t = -0.87$ ,  $p\text{-value} = 0.39$ ; females:  $\beta = -0.95 \pm 0.87$ ,  $N = 334$ ,  $t = -1.09$ ,  $p\text{-value} = 0.28$ ), making it unlikely that including arrival date would change our results.

Because naïve birds (which reproduce for the first time) and experienced birds (which reproduced at least once) differ in reproductive performance (Limmer & Becker, 2010), we added a binomial variable, "first reproduction (yes or no)" to our models of both annual local survival and breeding success. Moreover, because performance measures may be density-dependent (Szostek, Becker, Meyer, Sudmann, & Zintl, 2014), we added the annual number of breeding pairs as a covariate to all our breeders' models.

## 2.5 | Statistical analyses

### 2.5.1 | Fledging probability

To investigate whether the heterozygosity of hatchlings predicted their fledging probability, we used the fledging success (dead or fledged) of all genotyped hatchlings (as a dependent variable and heterozygosity,  $H_{s_{obs}}$  as both a linear and a quadratic explanatory variable in a generalized linear mixed model (GLMM) with a "logit" link function and a variance given by a binomial distribution. BSHO was added as categorical variable, laying date of the first egg in of the clutch as a continuous variable. In addition to additive effects, we considered first-order interactions with  $H_{s_{obs}}$ . To account for shared family and annual environmental variation between chicks, we included year and nest identity (nested within year) as random effects.

### 2.5.2 | Local prospecting and recruitment probabilities

To investigate whether the heterozygosity of fledglings and prospectors predicted their local prospecting and recruitment probability,

respectively, we used the fate of the fledglings (prospecting locally or not) and prospectors (locally recruited as breeders or not) as dependent variables and the fledgling or prospector  $H_{s_{obs}}$  (linear and squared) as explanatory variables in two GLMMs with a "logit" link function and a variance given by a binomial distribution. Fledging mass was added as a continuous variable, sex as a two-level factor, because natal philopatry is known to be higher for males than females (Becker, Ezard, Ludwigs, Sauer-Gürth & Wink, 2008). For recruitment probability, we also added the annual number of breeding pairs and age at first prospecting as covariates. In addition to additive effects, we considered first-order interactions with  $H_{s_{obs}}$ . To account for shared family and annual environmental variation between chicks, we included year and nest identity (nested within year) as random effects. Fledging mass and age at first prospecting did not correlate with  $H_{s_{obs}}$  (fledging mass:  $\beta = 0.05 \pm 0.9$ ,  $N = 3,607$ ,  $t = 0.05$ ,  $p\text{-value} = 0.96$ ; age at first prospecting:  $\beta = -0.04 \pm 0.10$ ,  $N = 1,388$ ,  $Z = -0.36$ ,  $p\text{-value} = 0.72$ ), such that correcting for these variables cannot mask effects of  $H_{s_{obs}}$  on prospecting or recruitment probability.

### 2.5.3 | Annual local survival and breeding probability

To investigate whether heterozygosity predicted the local annual survival and breeding probability of recruits, we used their local annual survival or breeding status as a dependent variable and  $H_{s_{obs}}$  (linear and squared) as an explanatory variable in two GLMMs with a "logit" link function and a variance given by a binomial distribution. Age (linear and squared) and sex were entered as covariates (Zhang, Rebke, et al., 2015). We also accounted for whether a reproductive event was the first by adding a binomial variable "first reproduction (yes or no)" to our annual local survival model. We added the annual colony density as a covariate to both the annual survival and breeding probability models. In the GLMM for local annual breeding probability, AFR was added as an additional categorical variable. Additive effects of all these variables, as well as the first-order interactions with  $H_{s_{obs}}$  (linear and squared), were considered. Breeder identity and year were added as random effects to avoid pseudo-replication and account for environmental variation, respectively.

### 2.5.4 | Annual local reproductive success

A final model was run to investigate whether heterozygosity was related to reproductive success, assessed as the annual number of fledglings produced. Because male and female reproductive success are not independent, to avoid pseudo-replication and to maximize sample size for each analysis, we ran separate models for males and females (Bouwhuis et al., 2015). The number of fledglings was entered as a dependent variable and the adult breeder  $H_{s_{obs}}$  (linear and squared) as an explanatory variable in a GLMM with a "log" link function and a variance given by a Poisson distribution (appropriate for count data). Age (linear and squared) and AFR (categorical) were entered as additional explanatory

variables (Zhang, Rebke, et al., 2015). As in previous models, the variables “first reproduction (yes/no)” and annual colony density were added as well and additive effects of all variables, as well as the first-order interactions with  $H_{s_{obs}}$  (linear and squared), were considered, while breeder identity and year were added as random effects. To investigate at which reproductive stage the observed effect of heterozygosity originated, we repeated the minimal adequate model for annual fledgling production for two underlying traits: brood size (i.e., the number of chicks that hatched) and clutch size (i.e., the number of eggs laid) (also see Bouwhuis, Sheldon, Verhulst, & Charmantier, 2009).

To ensure that any effects of  $H_{s_{obs}}$  on reproductive success were not driven by effects in a few specific years only, we repeated the minimal adequate models for male and female fledgling production in a year-by-year analysis. These models were run for 2003–2016, with the exception of 2005, as the sample sizes prior to 2003 were very small ( $N \leq 8$ ) and because in 2005 the fledging success was very low (only four chicks fledged in the used data) due to intense owl predation. Details about these analyses are given in Supporting Information Appendix S2.

All models were run with R 3.4.2 (R Core Team, 2014) using the function “glmer” in the package “LME4” (Bates, Maechler, Bolker, & Walker, 2015). All continuous variables were standardized (by subtracting the mean of the variable from each value and dividing it by the squared variance of the variable). All full models were tested for overdispersion using the function “dispersion\_glmer” implemented in the package “BLMECO” (Korner-Nievergelt et al., 2015), and all ratios were below the recommended threshold of 1.40. Non-significant interactions and quadratic effects were removed following a backwards elimination procedure with the level of significance set to  $\alpha = 0.05$ . We, however, also used an information theoretic approach to select sets of plausible models and to estimate their relative importance using the Akaike information criterion corrected for small sample sizes (AICc) and the  $\Delta AICc$  to infer support for models in the candidate set (Burnham & Anderson, 2002; Burnham, Anderson, & Huyvaert, 2011). The details of this method and the associated results, which are very similar to those obtained with the backwards elimination procedure, are presented in Supporting Information Appendix S3. Parameter estimates are given as mean  $\pm$  SE.

### 2.5.5 | Local versus general effect

The mean inbreeding coefficient in our population ( $\pm SD$ ) was calculated using our microsatellites and the function “inbreeding” implemented in the R package “ADEGENET” (Jombart, 2008). The heterozygosity correlation across loci (i.e., identity disequilibrium) was evaluated using the  $g_2$  statistic (David et al., 2007), which measures the excess of double heterozygous at two loci relative to the expectation of random association (i.e., covariance in heterozygosity) standardized by the average heterozygosity (Szulkin et al., 2010). Identity disequilibrium is considered as the main cause of HFCs (Szulkin et al., 2010), such that a  $g_2$  significantly different from zero means that heterozygosity across loci correlates

with individual inbreeding, which increases the probability to detect HFCs (Szulkin et al., 2010). Our estimate of  $g_2$  was obtained using the R package “INBREEDR” (Stoffel et al., 2016) by running 1,000 bootstraps. The 95% confidence interval was defined using 1,000 permutations. Using the same package, we also estimated identity disequilibrium by dividing our 15 loci in two random subsets, testing the correlation in heterozygosity between the two subsets (heterozygosity–heterozygosity correlation, HHC) and repeating this 10,000 times, in order to obtain the HHC mean, SD and confidence interval at 95% (Balloux et al., 2004).

Although local effects would need to be substantial to be detected, we tested whether the effect of heterozygosity on fitness parameters (see Results) was associated with specific loci. To do so, we used likelihood ratio tests to compare our final models using  $H_{s_{obs}}$  against respective models with all 15 single loci (coded 0 for homozygous and 1 for heterozygous) fitted as simultaneous covariates (Kuepper et al., 2010; Phillips, Jorgensen, Jolliffe, & Richardson, 2017; Szulkin et al., 2010). In case of significance, this test would lend support to the local effect hypothesis.

## 3 | RESULTS

### 3.1 | Hatching to recruitment

The average  $H_{s_{obs}}$  of the 7,961 hatchlings, 3,612 fledglings and 1,388 prospectors was 0.9995 ( $\pm 0.002$ ), 0.9989 ( $\pm 0.003$ ) and 0.9990 ( $\pm 0.005$ ), respectively (Table 1). Variation in neither fledging nor local prospecting probability after fledging was explained by variation in  $H_{s_{obs}}$  (Tables 1 and 2). Local recruitment probability after prospecting, however, was positively correlated with  $H_{s_{obs}}$  (Tables 1 and 2, Figure 1).

### 3.2 | Breeders

The average  $H_{s_{obs}}$  of the 762 breeders was 1.0071 ( $\pm 0.006$ ) and not significantly different between the sexes ( $\beta = 0.004 \pm 0.01$ ,  $t = 0.34$ ,  $p = 0.74$ ): 1.0052 ( $\pm 0.008$ ) for the 426 males and 1.0095 ( $\pm 0.010$ ) for the 336 females (Table 1).

Variation in annual local survival probability was explained by an interaction between  $H_{s_{obs}}$  and the variable “first reproduction (yes or no)” (Table 3). This interaction showed that survival was highest for birds with an intermediate level of  $H_{s_{obs}}$  in the year following first reproduction, but was independent of  $H_{s_{obs}}$  in experienced breeders (Table 3).

There was no evidence for a correlation between  $H_{s_{obs}}$  and breeding probability (Table 3).  $H_{s_{obs}}$  was, however, significantly associated with the annual local number of fledglings produced in both males and females (Figure 2a, Table 3): fledgling production declined with heterozygosity in males, while females with an intermediate level of heterozygosity produced most fledglings. These significantly negative and quadratic effects of  $H_{s_{obs}}$  in males and females, respectively, were also significant when analysing variation in brood size (Figure 2b, Table 3), but non-significant at the level of clutch

size (Figure 2c, Table 3). Moreover, the effects were highly consistent across years, as indicated by an additional year-by-year analysis (Supporting Information Appendix S2).

### 3.3 | Local versus general effect

Based on the microsatellites, the average inbreeding coefficient in our colony was estimated at  $0.17 \pm 0.08$  (min = 0.06, max = 0.66). Heterozygosity was weakly, but significantly correlated across loci ( $g_2 = 0.0021$ ,  $n = 2,888$ , 95% CI = 0.0002–0.0039,  $p = 0.003$ ; average HHC =  $0.037 \pm 0.017$ , CI = 0.003–0.067). Comparisons between the single-locus models of local recruitment probability, male and female annual local reproductive success and the respective models using  $H_{s_{obs}}$  as a multilocus variable were non-significant (local recruitment probability:  $df = 14$ ,  $p = 0.47$ ; male annual local reproductive success:  $df = 14$ ,  $p = 0.57$ ; female annual local reproductive success:  $df = 14$ ,  $p = 0.49$ ), suggesting a general rather than a local effect.

## 4 | DISCUSSION

Using data from a 26-year longitudinal study of common terns, we found evidence for few, and small life stage- and sex-specific HFCs. In early life, heterozygosity was not correlated with fledging probability or local prospecting probability, but positively correlated with local recruitment probability. Among breeders, annual local survival was only correlated with heterozygosity in the year after first reproduction, with survival being highest for birds with an intermediate

level of  $H_{s_{obs}}$ . Although the probability to breed was not correlated with heterozygosity, annual local fledgling production was negatively correlated with heterozygosity in males and highest in intermediately heterozygous females. These latter associations partly arose from differential hatching success only, as clutch size was not correlated with parental heterozygosity, while brood size was.

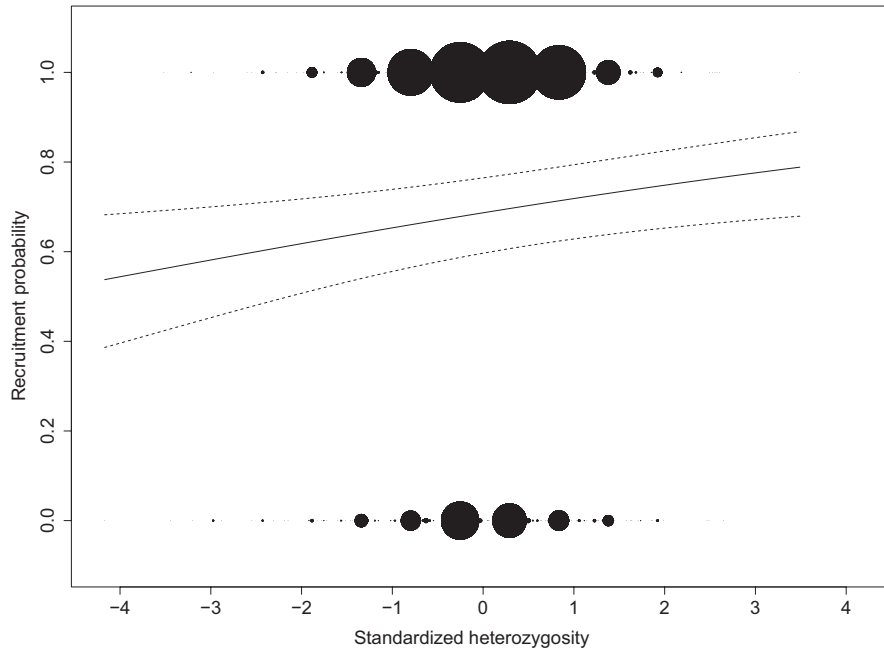
The few HFCs that were detected appear due to a low general genome-wide effect of heterozygosity, rather than an effect of the heterozygosity at specific loci (local effect) and the small, but significant,  $g_2$  value indicates that the markers we used provide information on inbreeding (Balloux et al., 2004; David et al., 2007). According to a meta-analysis conducted by Miller and Coltman (2014), our low  $g_2$  as well as low HHC values should indicate weak HFCs, which could be difficult to detect. Our number of microsatellite loci used (15) is low, but close to the average of other HFC studies (Chapman et al., 2009; Miller & Coltman, 2014), and our number of genotyped individuals ( $N = 7,974$ ) far exceeds the published range (7–1,055), such that our number of genotypes (7,974 individuals  $\times$  15 markers = 119,610 genotypes; Slate et al., 2004) is more than double the highest number of genotypes (573 individuals  $\times$  101 markers = 57,873 genotypes; Slate et al., 2004) of all studies reviewed in Chapman et al. (2009; also see Harrison et al., 2011; Judson, Knapp, & Welch, 2018; Monceau et al., 2013; Shaner et al., 2013; Soulsbury & Lebigre, 2018; Velando et al., 2015; Voegeli, Saladin, Wegmann, & Richner, 2012 for examples of more recent studies using a similar or even lower number of loci for estimating HFCs). The low number of loci used, associated with the weak HFCs detected, could prevent the detection of local effects (Szulkin et al., 2010), but, as also stated by Szulkin et al. (2010), although a larger number of loci provide a

**TABLE 2** Effects of observed heterozygosity ( $H_{s_{obs}}$ ), brood size/hatching order combinations, laying date, fledging mass, age at first prospecting and colony density on fledging probability, prospecting probability and recruitment probability, with parameter estimates as obtained from minimal adequate models and with significant effects ( $\alpha < 0.05$ ) in bold. “–” means a parameter was not fitted to the model

Dependent variable	Fledging probability (n = 7,961)			Prospecting probability (n = 3,607)			Recruitment probability (n = 1,388)		
	Estimate $\pm$ SE	Z value	p-value	Estimate $\pm$ SE	Z value	p-value	Estimate $\pm$ SE	Z value	p-value
Intercept	0.44 $\pm$ 0.27	1.62	0.11	<b>-0.45 <math>\pm</math> 0.17</b>	<b>-2.59</b>	<b>0.01</b>	<b>1.00 <math>\pm</math> 0.21</b>	<b>4.77</b>	<b>&lt;0.001</b>
$H_{s_{obs}}$	0.007 $\pm$ 0.03	0.27	0.79	0.007 $\pm$ 0.04	0.19	0.85	<b>0.15 <math>\pm</math> 0.06</b>	<b>2.64</b>	<b>&lt;0.01</b>
BSHO2.1 <sup>a</sup>	0.02 $\pm$ 0.11	0.14	0.89	–	–	–	–	–	–
BSHO2.2 <sup>a</sup>	<b>-0.98 <math>\pm</math> 0.11</b>	<b>-8.70</b>	<b>&lt;0.001</b>	–	–	–	–	–	–
BSHO3.1 <sup>a</sup>	0.11 $\pm$ 0.11	0.98	0.33	–	–	–	–	–	–
BSHO3.2 <sup>a</sup>	<b>-0.59 <math>\pm</math> 0.11</b>	<b>-5.44</b>	<b>&lt;0.001</b>	–	–	–	–	–	–
BSHO3.3 <sup>a</sup>	<b>-2.31 <math>\pm</math> 0.13</b>	<b>-18.45</b>	<b>&lt;0.001</b>	–	–	–	–	–	–
Laying date	<b>-0.28 <math>\pm</math> 0.03</b>	<b>-9.42</b>	<b>&lt;0.001</b>	–	–	–	–	–	–
Fledging mass	–	–	–	<b>0.25 <math>\pm</math> 0.04</b>	<b>6.40</b>	<b>&lt;0.001</b>	<b>0.14 <math>\pm</math> 0.06</b>	<b>2.24</b>	<b>0.02</b>
Sex(female)	–	–	–	-0.04 $\pm$ 0.07	-0.57	0.57	<b>-0.44 <math>\pm</math> 0.12</b>	<b>-3.69</b>	<b>&lt;0.001</b>
Age at 1st prospecting	–	–	–	–	–	–	-0.10 $\pm$ 0.06	-1.80	0.07
Colony density	–	–	–	–	–	–	-0.02 $\pm$ 0.19	-0.13	0.90
Marginal $R^2$	0.13			0.01			0.02		
Conditional $R^2$	0.31			0.11			0.11		

<sup>a</sup>Brood size (BS) and hatching order (HO) category.





**FIGURE 1** Association between observed heterozygosity ( $H_{s_{obs}}$ ) and local recruitment probability of local prospectors. Dots represent the observed local recruitment as a function of the standardized  $H_{s_{obs}}$ . Dot size is proportional to the number of local prospectors. Lines represent the model prediction (in bold) and its associated standard errors (dashed)

more precise inbreeding estimate, a lower number of markers should not be used as an argument to invalidate significant findings. Indeed, Forstmeier, Schielzeth, Mueller, Ellegren, and Kempenaers (2012) found that 11 microsatellites markers distributed across the zebra finch genome were as informative as 1,359 SNP markers or as a 5th generation pedigree. Similarly, Taylor et al. (2010) reported a significant correlation between pedigree-based inbreeding and a panel of 13 microsatellites.

Between hatching and local recruitment, common tern HFCs appeared to be life stage-dependent. For the earlier life stages (i.e., fledging probability and local prospecting probability), we did not observe any associations with heterozygosity. Non-significant HFCs can arise when there are too few microsatellite loci assessed that do not reflect genome-wide heterozygosity, which could be the case in our study. However, despite our relatively low number of loci, we found significant HFCs for later life stages and  $g_2$  and HHC values were significant. Alternatively, strong selection on a non-heterozygosity-related trait can mask any effect of heterozygosity if not corrected for (Annavi et al., 2014; Arct et al., 2017; Harrison et al., 2011, but see Ferrer, Garcia-Navas, Jose Sanz, & Ortego, 2016; Forcada & Hoffman, 2014; Lesbarreres, Primmer, Laurila, & Merila, 2005). In our colony, variation in fledging success is to a large extent explained by unpredictable and variable food supplies (Daenhardt & Becker, 2011; Vedder et al., 2019) and, owing to an efficient brood reduction strategy, hatchling mortality peaks within the first week of life and is strongly biased towards second and third hatchlings (Vedder et al., 2017). Moreover, fledging success covaries with laying date, such that hatchlings from earlier broods have an increased fledging probability. Here, we correct for these hatching order and laying date effects and show that heterozygosity, which does not differ between siblings of different hatching order ( $F_{4,4441} = 1.07$ ,  $p$ -value = 0.37) or vary with laying date ( $\beta = 0.49 \pm 0.47$ ,  $t = 1.05$ ,  $p$ -value = 0.30),

does not act as an additional cause of chick mortality. The period between fledging and prospecting acts as another strong selective phase (Braasch, Schaubroth, & Becker, 2009; Szostek & Becker, 2015). For this phase, we have so far found little evidence for individual-level determinants of survival: neither hatching order (Vedder et al. in revision), quality of the nest of origin (Vedder & Bouwhuis, 2018), nor hatching date, age at fledging or post-fledging departure date (Braasch et al., 2009) explained variation in prospecting probability. The only exception was a positive effect on prospecting and recruitment probability of fledging mass (this study) and last post-fledging mass (Braasch et al., 2009). However, prospecting probability also varied with cohort-level properties, namely the per-pair average number of fledglings produced (Vedder & Bouwhuis, 2018), colony size in the year of fledging (Szostek et al., 2014) and wintering conditions (Szostek & Becker, 2015). Perhaps survival from fledging to prospecting therefore is mostly determined by the environmental conditions a chick experiences before and after fledging (e.g., en route: Oppel et al., 2015; Rotics et al., 2016).

Because HFCs are expected to be strongest early in life (Koehn & Gaffney, 1984), many studies focused on early-life stages (Annavi et al., 2014; Arct et al., 2017; Hansson, Bensch, Hasselquist, & Akesson, 2001; but see Höglund et al., 2002; Taylor & Jamieson, 2007; Velando et al., 2015). The few studies that did investigate different age classes mostly compared young/juvenile stages versus adult stages (Canal et al., 2014; Cohas et al., 2009; Judson et al., 2018; Lieutenant-Gosselin & Bernatchez, 2006; Monceau et al., 2013; but see also Olano-Marin et al., 2011; Von Hardenberg et al., 2007) and most of them found contrasting heterozygosity effects between classes. Interestingly, these studies only detected significant HFCs at the juvenile stage, most likely due to the selective mortality of the most homozygous individuals at this stage, and therefore contrast with our own. In our study system, as

**TABLE 3** Effects of observed heterozygosity ( $H_{s_{obs}}$ ), age, sex, age at first reproduction (AFR), first reproduction (yes or no) and colony density on annual local survival, breeding probability and reproductive success (number of fledglings, brood size and clutch size), with parameters as obtained from minimal adequate models and with significant effects ( $\alpha < 0.05$ ) in bold. “\_” means a parameter was not fitted to the model

Data from	Local breeders (n = 762)						Male local breeders (n = 426)									
	Annual local survival probability			Annual local breeding probability			Annual number of fledglings			Annual brood size			Annual clutch size			
	Parameter	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value
Intercept	2.28 ± 0.14	15.94	<0.001	2.01 ± 0.75	2.69	0.01	0.39	0.39	0.39	0.39	-0.04 ± 0.41	-0.01	0.93	0.64 ± 0.28	2.29	0.02
$H_{s_{obs}}$	-0.01 ± 0.10	-0.07	0.95	-0.001 ± 0.13	-0.01	0.99	-0.09 ± 0.03	-2.95	<0.01	<0.01	-0.05 ± 0.02	-2.52	0.01	-0.01 ± 0.02	-0.81	0.42
$(H_{s_{obs}})^2$	0.08 ± 0.07	1.05	0.29	-	-	-	-	-	-	-	-	-	-	-	-	-
Age	-0.41 ± 0.14	-3.01	<0.01	-0.95 ± 0.14	-6.68	<0.001	0.44 ± 0.07	6.61	<0.001	<0.001	0.25 ± 0.05	4.67	<0.001	0.12 ± 0.04	2.63	<0.01
(Age) <sup>2</sup>	-	-	-	0.28 ± 0.08	3.32	<0.001	-0.16 ± 0.03	-4.58	<0.001	<0.001	-0.09 ± 0.02	-3.90	<0.001	-0.03 ± 0.02	-1.65	0.10
Sex (female)	0.19 ± 0.17	1.11	0.27	-0.06 ± 0.27	-0.23	0.82	-	-	-	-	-	-	-	-	-	-
AFR3	-	-	-	1.63 ± 0.70	2.32	0.02	0.12 ± 0.50	0.25	0.81	0.81	0.65 ± 0.41	1.59	0.11	0.30 ± 0.28	1.06	0.29
AFR4	-	-	-	1.75 ± 0.73	2.40	0.02	-0.01 ± 0.51	-0.02	0.98	0.98	0.67 ± 0.41	1.63	0.10	0.33 ± 0.28	1.17	0.24
AFR5+	-	-	-	1.80 ± 0.82	2.19	0.03	-0.08 ± 0.51	-0.16	0.87	0.87	0.65 ± 0.42	1.55	0.12	0.30 ± 0.29	1.05	0.29
First reproduction (yes)	0.29 ± 0.23	1.30	0.19	-	-	-	-0.11 ± 0.11	-0.99	0.32	0.32	-0.29 ± 0.07	-4.20	<0.001	-0.11 ± 0.05	-2.05	0.04
Colony density	0.08 ± 0.07	1.09	0.28	-0.07 ± 0.11	-0.66	0.51	0.09 ± 0.16	0.56	0.56	0.56	0.03 ± 0.05	0.65	0.52	0.01 ± 0.02	0.94	0.35
$H_{s_{obs}}$ : First reproduction (yes)	0.08 ± 0.15	0.51	0.61	-	-	-	-	-	-	-	-	-	-	-	-	-
$(H_{s_{obs}})^2$ : First reproduction (yes)	-0.28 ± 0.10	-2.74	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-
Marginal R <sup>2</sup>	0.02			0.03			0.03			0.08			0.03			
Conditional R <sup>2</sup>	0.13			0.26			0.14			0.11			0.03			
Data from	Female local breeders (n = 336)															
Dependent variable	Annual number of fledglings						Annual brood size						Annual clutch size			
Parameter	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	
Intercept	-0.58 ± 0.24	-2.45	0.01	0.52 ± 0.11	4.56	<0.001	0.89 ± 0.09	10.49	<0.001	0.89 ± 0.09	10.49	<0.001	0.64 ± 0.28	2.29	0.02	
$H_{s_{obs}}$	-0.01 ± 0.03	-0.32	0.75	0.003 ± 0.02	0.15	0.88	0.001 ± 0.02	0.06	0.95	0.001 ± 0.02	0.06	0.95	-0.01 ± 0.02	-0.81	0.42	
$(H_{s_{obs}})^2$	-0.04 ± 0.02	-2.12	0.03	-0.03 ± 0.01	-2.03	0.04	-0.01 ± 0.01	-1.18	0.24	-0.01 ± 0.01	-1.18	0.24	0.08 ± 0.04	2.28	0.02	
Age	0.25 ± 0.06	4.49	<0.001	0.17 ± 0.05	3.78	<0.001	0.08 ± 0.04	2.28	0.02	0.08 ± 0.04	2.28	0.02	-0.02 ± 0.01	-1.35	0.18	
(Age) <sup>2</sup>	-0.05 ± 0.02	-1.97	0.05	-0.05 ± 0.02	-2.55	0.01	-0.02 ± 0.01	-1.35	0.18	-0.02 ± 0.01	-1.35	0.18	-	-	-	-
Sex (female)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(Continues)

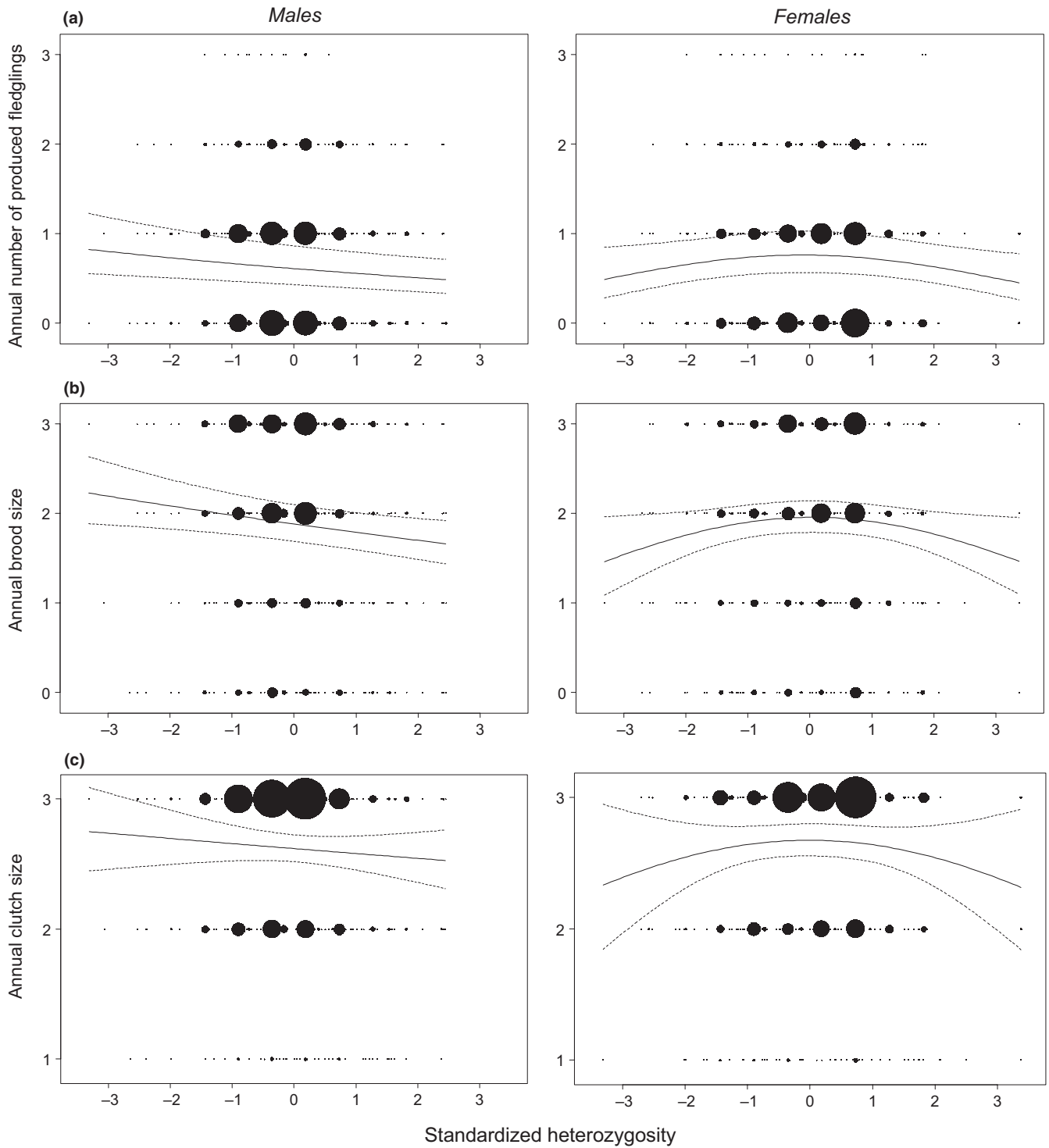
TABLE 3 (Continued)

Data from		Female local breeders (n = 336)									
Dependent variable	Parameter	Annual number of fledglings			Annual brood size			Annual clutch size			p-value
		Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	Estimate ± SE	Z value	p-value	
AFR3		0.23 ± 0.17	1.37	0.17	0.13 ± 0.11	1.26	0.21	0.08 ± 0.09	0.96	0.34	
AFR4		0.13 ± 0.18	0.72	0.47	0.16 ± 0.11	1.48	0.14	0.10 ± 0.09	1.06	0.29	
AFR5+		0.15 ± 0.21	0.68	0.50	0.15 ± 0.14	1.06	0.29	0.11 ± 0.12	0.96	0.34	
First reproduction (yes)		<b>-0.35 ± 0.12</b>	<b>-2.94</b>	<b>&lt;0.01</b>	<b>-0.39 ± 0.07</b>	<b>-5.19</b>	<b>&lt;0.001</b>	<b>-0.20 ± 0.06</b>	<b>-3.40</b>	<b>&lt;0.001</b>	
Colony density		-0.17 ± 0.10	-1.74	0.08	-0.02 ± 0.04	-0.38	0.71	0.01 ± 0.02	0.51	0.61	
Marginal R <sup>2</sup>		0.05			0.08			0.04			
Conditional R <sup>2</sup>		0.16			0.10			0.04			

explained above, early-life selection seems mostly stochastically environmentally determined. Such strong heterozygosity-independent selection before individuals start to reproduce may have allowed maintenance of a sufficient variability in prospector and breeder heterozygosity to detect HFCs. Indeed, a positive HFC was found in prospectors with respect to local recruitment probability. The most homozygous prospectors had a lower chance to recruit into the colony as breeders than the more heterozygous ones. The local prospectors which did not locally recruit can either have died or have recruited in another colony, two options that we unfortunately cannot distinguish. However, we would hypothesize that the observed heterozygosity-recruitment correlation could potentially be due to a negative heterozygosity-dispersal correlation. The importance of heterozygosity for dispersal decisions has been highlighted by theoretical studies (Motro, 1991; Roze & Rousset, 2009), but empirical studies are still rare (Gillingham, Cezilly, Wattier, & Bechet, 2013; Liebgold, Kramer, Roomian, Dolezar, & Cabe, 2018; Shafer, Poissant, Cote, & Coltman, 2011; Vanpé et al., 2015). In mountain goats (*Oreamnos americanus*, Shafer et al., 2011) and greater flamingos (*Phoenicopterus roseus*, Gillingham et al., 2013), however, heterozygosity was negatively correlated with dispersal, which supports the fitness-associated dispersal hypothesis (FAD, Hadany, Eshel, & Motro, 2004; Shafer et al., 2011). This hypothesis assumes that homozygous individuals are less competitive and more likely to disperse due to their lower capacity to acquire resources and/or mates. Our study population is indeed characterised by competition for access to partners, food and suitable places to breed (Becker, 2015; Becker et al., 2008; Szostek et al., 2014), such that the FAD hypothesis corroborates our results and may explain the positive correlation between heterozygosity and recruitment probability we observed. Studies tracking fledglings and subadults up to their recruitment would, however, be needed to more thoroughly assess this hypothesis.

Among breeders, our study revealed both a negative and two quadratic HFCs. In breeding males, fledgling production was negatively correlated with heterozygosity, indicating that homozygous males have a higher reproductive success. This pattern partly originated from homozygous males benefitting from an improved hatching success, but not from their partners producing larger clutches. Among females, we found reproductive success to be highest for individuals with intermediate levels of heterozygosity, a pattern which again originated partly during hatching. At present, we have no credible explanation for the differences in HFC between the sexes and between fitness components. We can only speculate on different selective processes being responsible for survival and reproduction between the sexes, but more work would be needed to identify such processes.

Overall, thanks to our large sample size and long-term study, we were able to assess heterozygosity-fitness correlations across life stages and the sexes. Our analyses revealed the existence of contrasting sex-specific and life stage-specific correlations and emphasize the importance of assessing fitness consequences across complete life histories when aiming to understand the selective process leading to evolutionary change.



**FIGURE 2** Associations between local breeder observed heterozygosity ( $H_{s_{obs}}$ ) and annual reproductive success in males (left) and females (right). Dots represent the observed number of fledglings (a), brood size (b) and clutch size (c) as a function of the standardized  $H_{s_{obs}}$ . Dot size is proportional to the number of local breeders. Lines represent the model predictions (bold) and their associated standard errors (dashed)

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#### DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.r236r31>.

#### AUTHORS' CONTRIBUTIONS

P.H.B. and M.W. designed the microsatellite study. P.H.B. and S.B. collected the field data. H.S.-G. performed the laboratory work. C.B. performed the genetic analyses. C.B., S.B. and O.V. designed the analytical framework and C.B. performed the statistical analyses. C.B. and S.B. co-wrote the manuscript with contributions from all co-authors.

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## SUPPORTING INFORMATION

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

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