Behav Ecol Sociobiol (2014) 68:1723–1731
DOI 10.1007/s00265-014-1780-1

ORIGINAL PAPER

Pairing patterns in relation to body size, genetic similarity and multilocus heterozygosity in a tropical monogamous bird species

Aurélie Quinard · François-Xavier Dechaume-Moncharmont · Frank Cézilly

Received: 25 April 2014 / Revised: 12 July 2014 / Accepted: 14 July 2014 / Published online: 8 August 2014

Abstract The relative influence of genetic and phenotypic quality on pairing status and mating patterns in socially monogamous species remains poorly documented. We studied social status and pairing patterns in relation to genetic similarity and multilocus heterozygosity (MLH) estimates from 11 microsatellite markers, and both tarsus length and wing chord (as a measure of competitive ability in territorial defence) in a socially monogamous tropical bird species where individuals defend territories year-round, alone or in pairs, the Zenaida dove, *Zenaida aurita*. Tarsus length and wing chord did not differ between unpaired territorial birds and paired ones in either sex, whereas paired females, but not paired males, tended to be more heterozygous than unpaired ones. Among 84 pairs, we found no evidence for assortative mating for tarsus length, wing chord, MLH or genetic similarity. However, within pairs, male wing chord was positively related to female MLH and female tarsus length was positively related to male MLH, with no evidence for local effects, suggesting assortative mating by individual quality. Although the observed pattern of mating in Zenaida doves may be the product of mutual mate choice, further assessment of this hypothesis requires direct investigation of both mating preference in each sex and lifetime reproductive success in relation to body size and MLH.

Keywords Assortative mating · Mate choice · Heterozygosity · Wing chord · *Zenaida aurita* · Zenaida dove

Communicated by M. Hughes

A. Quinard · F.-X. Dechaume-Moncharmont · F. Cézilly
UMR CNRS 6282 Biogéosciences, Université de Bourgogne,
6 boulevard Gabriel, 21000 Dijon, France

F. Cézilly (✉)
Institut Universitaire de France, Paris, France
e-mail: frank.cezilly@u-bourgogne.fr

Introduction

In monogamous species with biparental care, both males and females are expected to exert mate choice (Jones and Hunter 1993; Johnstone et al. 1996). Mutual mate choice can have contrasted outcomes at the population level, however, depending on whether individuals express preference for absolute or relative individual quality, or a combination of both. In the former case, positive assortative mating should occur when the relationship between individual quality and phenotypic or genotypic characters does not differ between sexes. In the case of a relative preference, assortative mating will be positive if individuals express a homotypic preference, and conversely, negative if individuals prefer individuals who are dissimilar to themselves as reproductive partners (Cézilly 2004). Preference for dissimilar mates may be linked to direct benefits if complementarity between mates depends on their degree of phenotypic dissimilarity (see for instance Marzluff and Balda 1988) or to indirect benefits in the case of genetic compatibility (Tregenza and Wedell 2000). Finally, there may be no simple match between male and female phenotypes or genotypes, even though pairing occurs between individuals of similar quality, if the traits linked to individual quality are sex-specific (Faivre et al. 2001) or if individuals of each sex combine criteria for absolute and relative quality differently (Thünken et al. 2012).

Individual quality can influence both access to a mate and mate quality, such as low-quality individuals would remain unpaired and high-quality ones would be paired between themselves. Positive assortative mating for various phenotypic traits potentially indicative of individual quality, such as body size (Helfenstein et al. 2004; Haggerty 2006; Grant and Grant 2008), ornaments (Andersson et al. 1998; Regosin and Pruett-Jones 2001; Jawor et al. 2003; Row and Weatherhead 2011) or age (Cézilly et al 1997; Fasola et al. 2001) have been regularly observed in monogamous species. Parallel to this, there is growing piece of evidence for assortative mating based on absolute or relative genetic quality among monogamous species, depending on whether individuals look for good genes or genetic complementarity (Mays et al. 2008). One particular aspect of absolute genetic quality in diploid organisms is heterozygosity. In various species, including monogamous ones, individual quality is positively related to heterozygosity at one or several loci (Hansson and Westerberg 2002; Kempenaers 2007; Chapman et al. 2009). According to the heterozygosity theory (Brown 1997; but see Aparicio 2011), choosing a heterozygous mate could bring direct benefits to the individual and its offspring. Accordingly, positive assortative mating for heterozygosity estimated from neutral or selected markers has been reported in a few monogamous species (Bonneaud et al. 2006; Garciá-Navas et al. 2009; Ortego et al. 2009). Alternatively, individuals may select genetically dissimilar mates to increase offspring heterozygosity. Again, some evidence exists in socially monogamous species for negative assortative mating in relation to genetic similarity based on neutral (Mulard et al. 2009; but see Cohen and Dearborn 2004) or functional markers (Freeman-Gallant et al. 2003; Juola and Dearborn 2012; but see Sommer 2005; Knafler et al. 2012).

So far, few studies have considered simultaneously the genetic and phenotypic dimensions of individual quality in relation to pairing patterns in socially monogamous species (but see Freeman-Gallant et al. 2003; García-Navas et al. 2009; Thünken et al. 2012). In particular, heterozygosity can influence body size in vertebrates (Hoffman et al. 2010; Herdegen et al. 2013), such that patterns of assortative mating in relation to both parameters might be more complex than previously thought. Here, we analyse variation in social status and patterns of mating in relation to body size (as assessed from wing chord and tarsus length), heterozygosity and genetic similarity between mates in the Zenaida dove, *Zenaida aurita*. In this tropical monogamous bird species, with continuous breeding and year-long pair bonds, most individuals defend, alone or in pairs, all-purpose territories against conspecifics (Wiley 1991; Quinard and Cézilly 2012). Males are on average 4–5 % larger and heavier than females (Dechaume-Moncharmont et al. 2011), and although both partners take part in territorial defence, males are generally more involved than females in deterring conspecific intruders (Quinard and Cézilly 2012). In particular, aggressive interactions between individuals can escalate to wing displays (when an individual spreads its wing contralaterally to its adversary), eventually followed by sharp wing slaps on the opponent (Quinard and Cézilly 2012), suggesting that wing length could be an honest signal of male quality. The species is further characterised by year-round breeding and multiple nesting attempts, with some pairs rising up to four broods per year (Wiley 1991). Interestingly, female heterozygosity has been found to influence fecundity and/or egg size in several bird species (Ortego et al. 2007; Tomiuk et al. 2007; Garcia-Navas et al. 2009; Olano-Marin et al. 2011; Wetzel et al. 2012), and larger females have been found to have reduced inter-clutch intervals in columbids (Johnson and Johnston 1989). Therefore, male Zenaida doves might benefit from pairing with more heterozygous and larger females.

Materials and methods

Study species and population

The Zenaida dove is a socially monogamous and granivorous bird species (Wiley 1991), which is abundant over much of its distribution range, from the tip of the Yucatan peninsula to the south of the Caribbean area (Bond 1993). Although the traditional habitat of the Zenaida dove corresponds to open woodlands and secondary forests, on several islands, it can be found in large numbers in cultivated fields, gardens and urbanised areas (Wiley 1991; Sol et al. 2005). Zenaida doves feed on the ground primarily alone or in pairs, but on some islands, they can form large foraging groups where food is particularly abundant (Sol et al. 2005; Monceau et al. 2011). Paired individuals breed year-round, with a peak in reproductive activity from January to April (Wiley 1991; FC personal observation) and can maintain pair bonds over several years (FC, unpublished data). Individuals benefit from pair bonding through shared territorial defence (Quinard and Cézilly 2012) and reduced anti-predator vigilance while feeding (Cézilly and Keddar 2012).

General field methods and status determination

We conducted banding of a population of Zenaida doves on the west coast of Barbados, around the city of Holetown (13° 10′ 60 N, 59° 38′ 60 W) between 2007 and 2013. The study area consisted of recreational and residential areas, including private villas with gardens, some parks with planted trees and modest malls. We trapped birds using walk-in baited traps and clap-nets. Each captured bird was equipped with an aluminium ring from the Museum National d'Histoire Naturelle (Paris, France) engraved with a reference number and a unique combination of coloured plastic rings. In addition, we took morphometric measurements (tarsus length and wing chord) as well as a blood sample (40 μl) allowing subsequent molecular sexing and microsatellite genotyping (see Monceau et al. 2011 for details).

Each year since 2007, regular monitoring of the ringed population of Zenaida doves using binoculars has been carried out during the February–May period and since 2008, during the November–December period. We used repeated observations of the marked birds to ascertain social status. An unpaired territorial individual was a male or a female that solitarily defended a territory. Note, however, that unpaired territorial individuals can correspond either to individuals that have failed to attract a partner on their territory or to widowed birds which have kept their territory following the death of their mate and have not yet remated. Indeed, anecdotal evidence (FC personal observation) indicates that both male and female widowed birds can remain single on their territory for up to 10 months following the disappearance of their mate. A territorial pair consisted of a male and a female that both attended a common territory that they defended against conspecific intruders (Sol et al. 2005; Quinard and Cézilly 2012) and where they courted and copulated. In most cases of mate-switching observed during the study period, the former partner had disappeared and was never seen again, although in a few cases, divorce had occurred. In order to avoid pseudo-replication in the analysis of assortative pairing, we used for each individual observed with more than one partner the pair with the longest known duration of pair bonds.

Genotyping, individual heterozygosity and relatedness estimates

We genotyped all individuals at 16 polymorphic microsatellite markers developed for the Zenaida dove (Monceau et al 2009). The full laboratory protocol applied to genotype individuals is described in Monceau et al. (2009). Loci were tested for Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using GENEPOP (v. 4.1.4.; Rousset 2011).

Various estimates of multilocus heterozygosity have been proposed (see review in Chapman et al. 2009). Following recommendations by Szulkin et al. (2010), we favoured the use of the multilocus heterozygosity (MLH) index to calculate individual heterozygosity. The MLH index ranges from 0 (when all loci are homozygous) to 1 (when all loci are heterozygous), with higher values corresponding to higher heterozygosity. However, we also estimated HL (Aparicio et al. 2006) to test the sensitivity of the models to the choice of heterozygosity measure. Calculations were made using the package Rhh (Alho et al. 2010) for R (v. 3.0; R Core Team 2013).

Following recommendations from Szulkin et al. (2010), we measured identity disequilibrium, as the excess of double heterozygous genotypes at two loci relative to the expectation of random association (i.e. covariance in heterozygosity) standardised by average heterozygosity. To that end, we computed parameter g_2 and tested whether this parameter differed significantly from zero using the method proposed by David et al. (2007), as implemented in the Robust Multilocus Estimate of Selfing (RMES) software (available at http://www.cefe.cnrs.fr/en/genetique-et-ecologie-evolutive/patrice-david), with 10,000 iterations. In large populations subject to inbreeding, parameter g_2 is expected to be constant for any pair of loci considered and only depends on the mean and variance of inbreeding in the population (David et al. 2007).

We estimated genetic similarity between male in female in each pair using program SPAGeDi 1.0 (Hardy and Vekemans 2002), using the ‘two-gene’ relationship coefficient, *r*, described in Queller and Goodnight (1989). We therefore obtained a measure of genetic similarity between two mates based on allele sharing, with the influence of each allele being weighed by its frequency in the population.

Statistical analyses

We first used GLMs to analyze the relationship between wing chord and tarsus length, as well as the relationship between each morphometric variable and MLH, using each time sex as covariate (Husseneder and Simms 2008; Shaner et al. 2013). We then used logistic regressions to test for the effects of tarsus length, wing chord and MLH, and those of all the interactions between these three variables, on social status (coded as a binomial variable, i.e. unpaired vs paired).

We tested the hypothesis that Zenaida doves avoided mating with genetically similar individuals by checking whether the mean value of the two-gene relationship coefficient, *r*, (Queller and Goodnight 1989) in our sample of pairs laid outside the 95 % confidence interval of a distribution obtained under the assumption of random mating between all paired individuals of opposite sex using 10,000 iterations. In addition, we compared the observed genetic dissimilarity between each female and its mate to the mean genetic dissimilarity obtained for that female under the assumption of random mating using a paired *t* test.

We assessed assortative mating for wing chord, tarsus length and MLH, as well as between MLH and morphometric variables using parametric or non-parametric correlation tests, depending on whether or not data were normally distributed. The possibility that significant correlations involving MLH were due to local effects (i.e. single-locus heterozygosity) was investigated using two-tailed *t* tests for continuous traits (wing chord, tarsus length). Significant *P* values were corrected for multiple comparisons using a Bonferroni procedure.

All descriptive statistics are given as standard deviation (SD) of the mean or median and interquartile range depending on whether the variable was normally distributed or not, except where indicated.

All tests were performed using the R software (v. 3.0; R Core Team 2013), with a type I error set at 0.05.

Results

Overall, we identified 31 unpaired territorial owners (15 males and 16 females), and 98 different pairs of doves during the study period. However, after correcting for individuals involved in more than one pair, the sample size was reduced to 84 pairs. Five microsatellite markers deviated from Hardy-Weinberg equilibrium (HWE), due to the presence of null alleles detected with MICRO-CHECKER (van Oosterhout et al. 2004). The eleven remaining markers passed the test for linkage disequilibrium (LD). The majority of individuals were genotyped at the 11 loci, except for 16 birds that were genotyped at 10 loci, three at 9 loci and two at only 8 loci. The number of alleles per locus ranged from 6 to 12, the mean being 9.18. No major difference in heterozygosity was observed among loci. Identity disequilibrium was low and did not differ from zero (g_2=0.0023, SD=0.0036, P=0.2258).

Neither MLH (Shapiro-Wilk test, W=0.9465, P<0.0001) or HL (W=0.9635, P<0.0001) were normally distributed, and both estimates were highly correlated (r_s=0.9671, 95 % CI=[0.952; 0.975], n=199, P<0.0001). Using one or the other estimate had no influence on the results. For the sake of simplicity, we present only results obtained using MLH. Results obtained using HL are available on request.

Among the 199 individuals, both tarsus length and wing chord were normally distributed (Shapiro-Wilk test, tarsus length W=0.9898, P=0.1687; wing chord W=0.9955, P=0.8171). There was a significant effect of the interaction between sex and tarsus length on wing chord ($F_{1,195}$=4.603, P=0.0331), suggesting that the relationship between wing chord and tarsus length differed between sexes. Indeed, wing chord increased with tarsus length in males ($F_{1,97}$=11.84, P=0.0009), whereas wing chord was independent of tarsus length in females ($F_{1,98}$=0.2855, P=0.5943).

Only sex had an influence on tarsus length ($F_{1,197}$=26.708, P<0.00001), whereas neither MLH ($F_{1,196}$=0.5586, P=0.4557) nor the interaction between sex and MLH ($F_{1,195}$=0.047, P=0.8277) had one. In contrast, the interaction between sex and MLH ($F_{1,195}$=4.1804, P=0.04224) had a significant influence on wing chord, indicating that the relationship between wing chord and MLH differed between sexes. Considering this relationship within each sex, there was only a tendency for wing chord to increase with MLH in females ($F_{1,98}$=3.4536, P=0.0661), whereas no such effect was observed in males ($F_{1,97}$=1.1565, P=0.2849).

Genetic and phenotypic influences on pairing status

Among females, tarsus length (GLM χ^2=2.07, df=1, P=0.1438) and wing chord (χ^2=0.34, df=1, P=0.56) had no effect on pairing status, while there was a tendency for heterozygosity to have a positive influence on the probability of being paired (χ^2=2.99, df=1, P=0.0839), all interactions being non-significant (P≥0.35 in all cases). Tarsus length, wing chord, or MLH had no influence on pairing status (P≥0.5170 in all cases) in males, and all interactions were again non-significant.

Evidence for assortative mating

Within the 84 pairs, both tarsus length (Pearson correlation coefficient, r=0.060, 95 % CI [−0.156; 0.271] n=84, P=0.5856) and wing chord (Pearson correlation coefficient, r=0.106, 95 % CI [−0.111; 0.313], P=0.3392) were unrelated between males and females. Similarly, we found no evidence for assortative mating for MLH within pairs (Spearman rank correlation coefficient, r_s=−0.088, 95 % CI [−0.299; 0.136], P=0.4260).

Relatedness values within pairs ranged from −0.451 to 0.687 such that some pairs consisted of genetically related individuals. However, we found no evidence for disassortative mating in relation to genetic similarity as the observed mean degree of genetic similarity within pairs (r=−0.008) did not lie outside of the 95 % confidence interval of the distribution obtained under the assumption of random mating ([−0.040; 0.024]). Similarly, when considered within each pair, genetic similarity between a female and her partner did not differ from values expected under random mating (paired t test, N=84, P=0.6426).

However, within pairs, male wing chord (r_s=0.2862, 95 % CI [0.0756; 0.482], n=84, P=0.0083; Fig. 1) but not male tarsus length (r_s=0.0404, 95 % CI [−0.179; 0.248], n=84, P=0.7155) was positively associated with female MLH. In addition, male MLH was positively associated with female tarsus length (r_s=0.2684, 95 % CI [0.0510; 0.468], n=84, P=0.0136; Fig. 2) but not with female wing chord (r_s=0.0176, 95 % CI [−0.188; 0.225], n=84, P=0.8734) within pairs. We found no evidence for single-locus effects as all t tests comparing the size of partners between homozygous and heterozygous individuals at each locus were not significant after Bonferroni correction (P>0.0045).

Discussion

We found that both multilocus heterozygosity and body size influenced pairing patterns in Zenaida doves. However, there was no simple match between male and female heterozygosities or between male and female body sizes. Instead, males with longer wing chords were paired with more heterozygous females, while more heterozygous males were paired with female with longer tarsus. This is, to our knowledge, the first documentation of a complex pattern of pairing involving both genotypic and phenotypic quality in a socially monogamous species. Although there was a tendency for wing chord to increase with MLH in females, overall, there was no clear effect of heterozygosity on body size in our sample of paired and unpaired birds. This is in accordance with a previous study that found no evidence for an effect of heterozygosity on either body size or fluctuating asymmetry in adult Zenaida doves from the same population, using a much larger sample

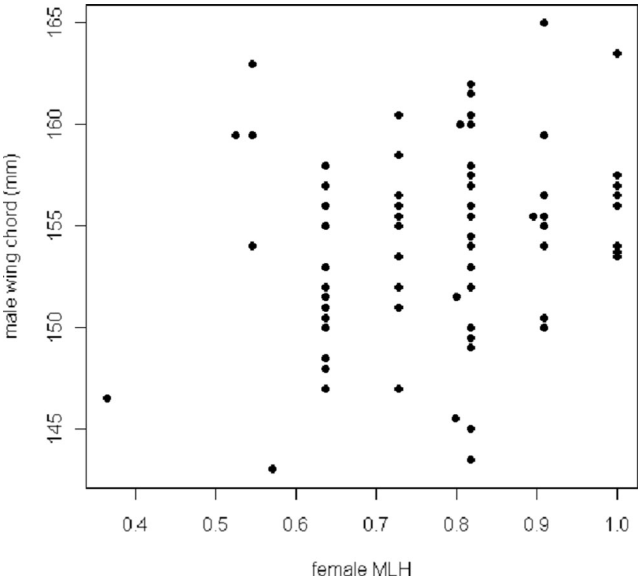

Fig. 1 Correlation between female MLH and male wing chord within pairs (n=84)

size (Monceau et al. 2013a) and suggests that the observed patterns of pairing were not influenced by a third association between heterozygosity and other variables related to individual quality.

Surprisingly, wing chord did not co-vary with tarsus length in females, whereas there was a positive correlation between the two variables in males. It has been argued that wing chord is not a representative measure of body size in birds, whereas tibiotarsus length would be more reliable (Rising and Somers 1989). However, we observed a strong correlation between the two traits in males, suggesting that the absence of relationship in females is rather due to some sex-specific effect. Indeed, the phenomenon could result from sex-related differences in the timing and/or extent of moult (Weimerskirch 1991; Svensson and Nilsson 1997; Hemborg and Merrilä 1998). However, such differences are generally observed in species showing a marked sexual dimorphism and tend to be absent or negligible in species with a reduced one (Alonso et al. 2009). In addition, temperate species tend to concentrate their moult in a few weeks (Ginn and Melville 1983), whereas moult in tropical species can spread over several months and overlap with breeding (Wyndham 1986; Tidemann and Woinarski 1994), possibly as an adaptive strategy for non-migratory individuals living in habitats with sufficient and constant food supply to allow year-round breeding (Foster 1974; Barta et al. 2006; Echeverry-Galvis and Hau 2012). Unfortunately, no detailed information about patterns of moult in the Zenaida dove is available. However, Grilli and Montalti (2010) found that the mass of primary feathers relative to body mass was higher in males than in females in the closely related eared dove, *Zenaida auriculata* who shares similar territorial behaviour. One possibility is that because of different roles in territorial defence (Quinard and Cézilly 2012), natural selection has favoured wing size as an honest signal of body size and, hence, competitive ability in male Zenaida doves, but not in females. More detailed data will however be needed to assess the generality and biological significance of the observed difference in the relation between wing size and tarsus length between males and females.

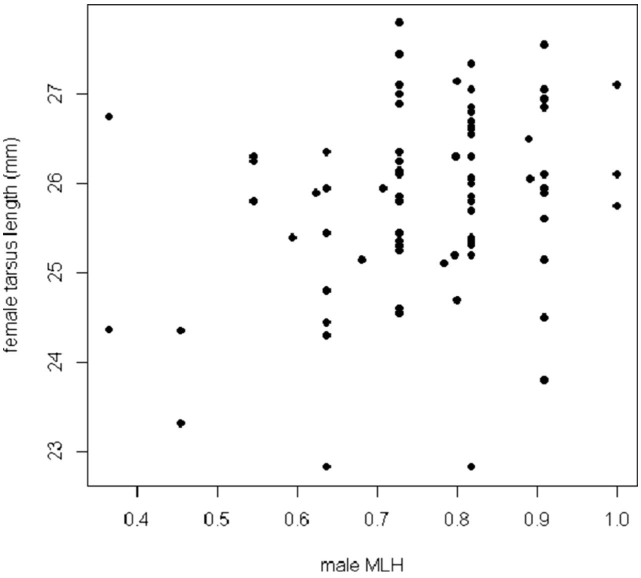

Fig. 2 Correlation between male MLH and female tarsus length within pairs (n=84)

We found little evidence for an influence of body size or heterozygosity at neutral loci on pairing status in Zenaida doves, although there was a slight tendency for paired females to be more heterozygous than unpaired ones. Limited information exists on the influence of heterozygosity on pairing status in monogamous species. However, paired females were found to be more heterozygous than single females in the Formosan subterranean termite (*Coptotermes formosanus*), while there was no difference in heterozygosity between paired and single males (Husseneder and Simms 2008). The weak effect observed in the present study might be due to a relatively small sample size for unpaired females (n=16). In addition, the test was conservative as some unpaired females might have been widowed birds that had been previously paired. Additional data may then help to assess the exact influence of heterozygosity on female pairing status in the future.

There was no evidence for size-asortative mating for body size, as neither tarsus length nor wing chord were correlated within pairs. A previous analysis on the same population, including a larger data set (Monceau et al. 2011; see also Sol et al. 2005), found that territorial individuals had longer wing chords than non-territorial ones (floaters), irrespective of their sex. This, together with direct observations on territorial defence (Quinard and Cézilly 2012), suggests that wing chord might be important to acquire and defend a territory. Still, we found no evidence for an effect of wing size on pairing status or for size-assortative mating based on wing chord. On the other hand, although size-assortative mating has been observed in various bird species (Wagner 1999; Delestrade 2001; Helfenstein et al. 2004; Einoder et al. 2008; Ledwon 2011), evidence for assortative mating based on wing size is limited (Haggerty 2006; Moreno-Rueda 2006). In addition, in the particular case of Zenaida doves, females play only a moderate role in territorial defence when paired (Quinard and Cézilly 2012), such that female wing chord might not represent a target for male mate choice, whereas the reverse might be true.

Contrary to two previous studies that reported significant and positive within-pair correlations between male and female heterozygosities in two different bird species (García-Navas et al. 2009; Ortego et al. 2009), we found no evidence for assortative mating for heterozygosity. Both in blue tits, *Cyanistes caeruleus*, (García-Navas et al. 2009) and in lesser kestrels (Ortego et al. 2009) positive assortative mating for heterozygosity appeared to confer both direct and indirect benefits. Egg production and quality increased with female heterozygosity, while more heterozygous males fed chicks at higher rates in blue tits (García-Navas et al. 2009), whereas clutch size increased with female heterozygosity and more heterozygous males tended to raise a larger number of fledglings in lesser kestrels (Ortego et al. 2007, 2009). In addition, in both species, mating with heterozygous individuals appeared to increase offspring heterozygosity (García-Navas et al. 2009; Ortego et al. 2009). Interestingly, a recent study (Monceau et al. 2013a) reported some evidence for outbreeding rather than inbreeding depression affecting chick body condition in our study population, such that pairs of Zenaida doves may not benefit from maximizing offspring heterozygosity. This may also explain why we found no evidence for an influence of genetic similarity between mates on pairing patterns, unlike what can be observed in socially monogamous species where deleterious effects of offspring homozygosity exist (Mulard et al. 2009).

In contrast, more heterozygous females were paired with males with longer wing chord and more heterozygous males were paired with female with longer tarsus length, whereas in each case, the reverse was not true. The strengths of the correlations was observed in the present study compared with effect sizes reported in other studies showing assortative mating for wing size (Haggerty 2006) or heterozygosity (García-Navas et al. 2009; Ortego et al. 2009) in birds. However, since male heterozygosity and wing chord were not correlated among males and tarsus length was unrelated to heterozygosity in both sexes, the observed mating patterns cannot be interpreted as indirect evidence for simple size-assortative mating. The observed pattern of mating in Zenaida doves may then support the idea that both body size and heterozygosity influence pairing patterns in the Zenaida dove, possibly through a directional preference for more heterozygous and/or larger individuals. Alternatively, low-quality individuals may prefer to mate between themselves if competition for mates is costly (see Fawcett and Johnstone 2003). Experimental evidence shows that low-quality female zebra-finches, *Taeniopygia guttata*, express preference for low-quality males as reproductive partners (Holveck and Riebel 2010). Experiments directly assessing male and female mate choice in relation to heterozygosity and body size in Zenaida doves may then be a useful complement to the present study.

The absence of local effects of heterozygosity seems to be in contradiction with the fact that identity desiquilibrium, i.e. the correlation of heterozygosity across all loci, did not differ from zero (Szulkin et al. 2010). However, inbreeding may create a correlation between fitness and heterozygosity, even with low g_2 (Szulkin et al. 2010), and recent evidence suggests that failing to detect identity disequilibrium should not be taken as evidence that inbreeding depression is absent (Kardos et al. 2014). In addition, a recent analysis on our study population (FC and R. Pradel, unpublished data) showed that multilocus heterozygosity has a positive effect on adult survival in our study population. One possibility, recently advanced by Wetzel et al. (2012), is that inbreeding may have occurred as a result of a bottleneck during colonization of the island, thus resulting in associations between alleles across loci that persisted until present time. The island of Barbados was formed approximately 700,000 YBP by tectonic uplift and was then colonised by birds via natural invasion from the much older Lesser Antillean volcanic islands (Lovette et al. 1999). However, a recent study (Monceau et al. 2013b) found no evidence for genetic bottleneck in the Barbados population of Zenaida doves. Alternatively, inbreeding might exist at a reduced spatial scale if individuals do not disperse far away from their natal territories. Indeed, limited dispersal is supposed to result in close spatial associations between relatives, thus resulting in a fine-scale genetic structure. Although it is generally considered that gene flow is less restricted in populations of birds compared to other vertebrates because of their higher dispersal capacity, this is not necessary true of populations living on relatively isolated small islands. Indeed, recent analyses (Monceau et al. 2013b) show very limited contemporary gene flow between Barbados and other islands in the Lesser Antilles. In addition, although sex-biased dispersal can limit inbreeding in a large number of bird species (Greenwood 1980), evidence exists for non-independent male and female sibling dispersal in some bird species (Alberico et al. 1992; Matthysen et al. 2005). Analysis of post-natal dispersal and settlement patterns of Zenaida doves banded as young may indicate to what extent this is true in our study population.

Overall, although direct evidence for active and rational choice is still lacking (Bateson and Healy 2005; Reaney 2009; Dechaume-Moncharmont et al. 2013), our results suggest that body size and heterozygosity may affect mutual mate choice in Zenaida doves, although not necessarily in the same fashion. In addition, our results indicate that patterns of mating in relation to absolute and relative genetic quality may vary depending on how heterozygosity affects fitness in natural populations. In that respect, studying bird species living in tropical islands with year-long reproduction and reduced gene flow might be of interest to provide a more comprehensive view of the causes and consequences of mutual mate choice in socially monogamous species (see Macedo et al. 2008; Stutchbury and Morton 2008).

Acknowledgments We thank three anonymous referees for very helpful comments on an earlier version. We are particularly grateful to Mr. Steve Devonish, Director of Natural Heritage, and Kim Downes Agard for granting us the permission to capture and ring Zenaida doves and to Cyril Bhola for hospitality. We thank Karine Monceau, Nicole Atherley, Laurent Brucy, Carla Daniel, Jérôme Moreau and Sébastien Motreuil, for their help in catching and banding birds, and Christine Dubreuil and Maria Gaillard for their help in genotyping. Patrice David provided very helpful comments on the manuscript. The study was funded by the Agence Nationale pour la Recherche (ANR, Programme Blanc "Monogamix") and the Conseil Régional de Bourgogne. AQ was supported by a doctoral grant from the Ministère de l'Enseignement Supérieur et de la Recherche.

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

Ethical standards Research was conducted under permit from the National Heritage Department (Division of Ministry of Environment and Drainage of Barbados). The experiments comply with the current laws of Barbados.

References

Alberico JAR, Reed JM, Oring LW (1992) Nonrandom philopatry of sibling spotted sandpipers *Actitis macularia*. Ornis Scand 23:504–508

Alho JS, Välimäki K, Merilä J (2010) Rhh: an R extension for estimating multilocus heterozygosity and heterozygosity-heterozygosity correlation. Mol Ecol Resour 10:720–722

Alonso H, Matias R, Granadeiro JP, Catry P (2009) Moult strategy of Cory's shearwaters *Calonectris diomedea borealis*: the influence of colony location, sex and individual breeding status. J Ornithol 150:329–337

Andersson S, Örnborg J, Andersson M (1998) Ultraviolet sexual dimorphism and assortative mating in blue tits. Proc R Soc Lond B 265:445–450

Aparicio JM (2011) The paradox of the resolution of the lek paradox based on mate choice for heterozygosity. Anim Behav 81:1271–1279

Aparicio JM, Ortego J, Cordero PJ (2006) What should we weigh to estimate heterozygosity, alleles or loci? Mol Ecol 15:4659–4665

Barta Z, McNamara JM, Houston AI, Weber TP, Hedenström A, Feró O (2006) Optimal moult strategies in migratory birds. Philos Trans R Soc Lond B 363:211–229

Bateson M, Healy SD (2005) Comparative evaluation and its implication for mate choice. Trends Ecol Evol 20:659–664

Bond J (1993) A field guide to the birds of the West Indies. Houghton Mifflin Harcourt, Boston

Bonneaud C, Chastel O, Federici P, Westerdahl H, Sorci G (2006) Complex Mhc-based mate choice in a wild passerine. Proc R Soc Lond B 273:1111–1116

Brown JL (1997) A theory of mate choice based on heterozygosity. Behav Ecol 8:60–65

Cézilly F (2004) Assortative mating. In: Mark Bekoff (ed) Encyclopedia of animal behavior Greenwood Pres, Westport, pp 876-881

Cézilly F, Keddar I (2012) Vigilance and food intake rate in paired and solitary Zenaida doves *Zenaida aurita*. Ibis 154:161–166

Cézilly F, Boy V, Tourenq C, Johnson AR (1997) Age-assortative pairing in the Greater Flamingo, *Phoenicopterus ruber roseus*. Ibis 139:331–336

Chapman JR, Nakagawa S, Coltman DW, Slate J, Sheldon BC (2009) A quantitative review of heterozygosity-fitness correlations in animal populations. Mol Ecol 18:2746–2765

Cohen LB, Dearborn DC (2004) Great frigatebirds, *Fregata minor*, choose mates that are genetically similar. Anim Behav 68:1229–1238

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

David P, Pujol B, Viard F, Castella V, Goudet J (2007) Reliable selfing rate estimates from imperfect population genetic data. Mol Ecol 16:2474–2487

Dechaume-Moncharmont FX, Monceau K, Cézilly F (2011) Sexing birds using discriminant function analysis: a critical appraisal. Auk 126:78–86

Dechaume-Moncharmont FX, Freychet M, Motreuil S, Cézilly F (2013) Female mate choice in convict cichlids is transitive and consistent with a self-referent directional rule. Front Zool 10:69

Delestrade A (2001) Sexual size dimorphism and positive assortative mating in Alpine choughs (*Pyrrhocoraxg raculus*). Auk 118:553–556

Echeverry-Galvis MA, Hau M (2012) Molt–breeding overlap alters molt dynamics and behavior in zebra finches, *Taeniopygia guttata castanotis*. J Exp Biol 215:1957–1964

Einoder LD, Page B, Goldsworthy SD (2008) Sexual size dimorphism and assortative mating in the short-tailed shearwater *Puffinus tenuirostris*. Mar Ornithol 36:167–173

Faivre B, Préault M, Théry M, Secondi J, Patris B, Cézilly F (2001) Breeding strategy and morphological characters in an urban population of blackbirds, *Turdus merula*. Anim Behav 61:969–974

Fasola M, Zhang YM, Zhao DQ, Dong YH, Wang H (2001) Age-assortative mating related to reproductive success in Black-crowned Night Herons. Waterbirds 24:272–276

Fawcett TW, Johnstone RA (2003) Mate choice in the face of costly competition. Behav Ecol 14:771–779

Foster M (1974) A model to explain molt-breeding overlap and clutch size in some tropical birds. Evolution 28:82–190

Freeman-Gallant CR, Meguerdichian M, Wheelwright NT, Sollecito SV (2003) Social pairing and female mating fidelity predicted by restriction fragment length polymorphism similarity at the major histocompatibility complex in a songbird. Mol Ecol 12:3077–3083

García-Navas V, Ortego J, Sanz JJ (2009) Heterozygosity-based assortative mating in blue tits (*Cyanistes caeruleus*): implications for the evolution of mate choice. Proc R Soc Lond B 276:2931–2940

Ginn HB, Melville DS (1983) Moult in birds. BTO Guide 19, Tring, UK

Grant PR, Grant BR (2008) Pedigrees, assortative mating and speciation in Darwin's finches. Proc R Soc Lond B 275:661–668

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Grilli MG, Montalti D (2010) On the study of the birds' plumage: the case of the Eared Dove (*Zenaida auriculata*). Rev Brasil Ornitol 18:341–343

Haggerty TM (2006) Sexual size dimorphism and assortative mating in Carolina Wrens. J Field Ornithol 77:259–265

Hansson B, Westerberg L (2002) On the correlation between heterozygosity and fitness in natural populations. Mol Ecol 11:2467–2474

Hardy OJ, Vekemans X (2002) SPAGEDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Mol Ecol Notes 2:618–620

Helfenstein F, Danchin E, Wagner RH (2004) Assortative mating and sexual size dimorphism in Black-legged Kittiwakes. Waterbirds 27:350–354

Hemborg C, Merilä J (1998) A sexual conflict in collared flycatchers. Proc R Soc Lond B 265:2003–2007

Herdegen M, Nadachowska-Brzyska K, Konowalik A, Babik W, Radwan J (2013) Heterozygosity, sexual ornament and body size in the crested newt. J Zool 291:16–153

Hoffman JI, Hanson N, Forcada J, Trathan PN, Amos W (2010) Getting long in the tooth: a strong positive correlation between canine size and heterozygosity in Antarctic fur seals *Arctocephalus gazella*. J Hered 101:527–538

Holveck M-J, Riebel K (2010) Low-quality females prefer low-quality males when choosing a mate. Proc R Soc Lond B 277:153–160

Husseneder C, Simms DM (2008) Size and heterozygosity influence partner selection in the Formosan subterranean termite. Behav Ecol 19:764–773

Jawor JM, Linville SU, Beall SM, Breitwisch R (2003) Assortative mating by multiple ornaments in northern cardinals (*Cardinalis cardinalis*). Behav Ecol 14:515–520

Johnson SG, Johnston RF (1989) A multifactorial study of variation in interclutch interval and annual reproductive success in the feral pigeon, *Columbia livia*. Oecologia 80:87–92

Johnstone RA, Reynolds JD, Deutsch JC (1996) Mutual mate choice and sex differences in choosiness. Evolution 50:1382–1391

Jones IL, Hunter FM (1993) Mutual mate choice in a monogamous seabird. Nature 362:238–239

Juola FA, Dearborn DC (2012) Sequence-based evidence for major histocompatibility complex-disassortative mating in a colonial seabird. Proc R Soc Lond B 279:153–162

Kardos M, Allendorf FW, Luikart G (2014) Evaluating the role of inbreeding depression in heterozygosity-fitness correlations: how useful are tests for indentity disequilibrium? Mol Ecol Resour 14:519–530

Kempenaers B (2007) Mate choice and genetic quality: a review of the heterozygosity theory. Adv Stud Behav 37:189–278

Knafler GJ, Clark JA, Boersma PD, Bouzat JL (2012) MHC diversity and mate choice in the Magellanic Penguin, *Spheniscus magellanicus*. J Hered 103:759–768

Ledwon M (2011) Sexual size dimorphism, assortative mating and sex identification in the whiskered tern *Chlidonias hybrida*. Ardea 99:191–198

Lovette IJ, Seutin G, Ricklefs RE, Bermingham E (1999) The assembly of an island fauna by natural invasion: sources and temporal patterns in the avian colonization of Barbados. Biol Inv 1:33–41

Macedo RH, Karubian J, Webster MS (2008) Extrapair paternity and sexual selection in socially monogamous birds: are tropical birds different? Auk 125:769–777

Marzluff JM, Balda RP (1988) Pairing patterns and fitness in a free-ranging population of pinyon jays: what do they reveal about mate choice? Condor 90:201–213

Matthysen E, Van de Casteele T, Adriaensen F (2005) Do sibling tits (*Parus major*, *P. caeruleus*) disperse over similar distances and in similar directions? Oecologia 143:301–307

Mays HL Jr, Alrecht T, Liu M, Hill GE (2008) Female choice for genetic complementarity in birds: a review. Genetica 134:147–158

Monceau K, Gaillard M, Harrang E, Santiago-Alarcon D, Parker P, Cézilly F, Wattier R (2009) Twenty-three polymorphic microsatellite markers for the Caribbean endemic Zenaida dove, *Zenaida aurita*, and its conservation in related Zenaida species. Conserv Genet 10:1577–1581

Monceau K, Wattier R, Dechaume-Moncharmont F-X, Motreuil S, Cézilly F (2011) Territoriality vs. flocking in the Zenaida dove, *Zenaida aurita*: resource polymorphism revisited using morphological and genetic analyses. Auk 128:15–25

Monceau K, Cézilly F, Moreau J, Motreuil S, Wattier R (2013a) Genetic and morphological evidence suggests rapid differentiation between island populations of a Caribbean endemic bird species, the Zenaida dove, *Zenaida aurita*. PLoS ONE 8:e82189

Monceau K, Wattier R, Dechaume-Moncharmont F-X, Dubreuil C, Cézilly F (2013b) Heterozygosity-fitness correlations in adult and juvenile Zenaida doves, *Zenaida aurita*. J Hered 104:47–56

Moreno-Rueda G (2006) Sexual size dimorphism and assortative mating for morphological traits in *Passer domesticus*. J Ethol 24:227–230

Mulard H, Danchin E, Talbot SL, Ramey AM, Hatch SA, White JF, Helfenstein F, Wagner RH (2009) Evidence that pairing with genetically similar mates is maladaptive in a monogamous bird. BMC Evol Biol 9:147

Olano-Marin J, Mueller JC, Kempenaers B (2011) Correlations between heterozygosity and reproductive success in the blue tit (*Cyanistes caeruleus*): an analysis of inbreeding and single locus effects. Evolution 20:4028–4041

Ortego J, Calabuig G, Cordero PJ, Aparicio JM (2007) Egg production and individual genetic diversity in lesser kestrels. Mol Ecol 16:2383–2392

Ortego J, Calabuig G, Bonal R, Munoz A, Aparicio JM, Cordero PJ (2009) Temporal variation of heterozygosity-based assortative mating and related benefits in a lesser kestrel population. J Evol Biol 22:2488–2495

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic-markers. Evolution 43:258–275

Quinard A, Cézilly F (2012) Sex roles during conspecific territorial defence in the Zenaida dove, *Zenaida aurita*. Anim Behav 83:47–54

Reaney LT (2009) Female preference for male phenotypic traits in a fiddler crab: do female use absolute or comparative evaluation? Anim Behav 77:139–143

Regosin JV, Pruett-Jones S (2001) Sexual selection and tail-length dimorphism in scissor-tailed flycatchers. Auk 118:167–175

Rising JD, Somers KM (1989) The measurement of overall body size in birds. Auk 106:666–674

Rousset F (2011) Genepop 4.1 for Windows/Linux/Mac OS X, http://kimura.univ-montp2.fr/~rousset/Genepop.htm

Row KMC, Weatherhead PJ (2011) Assortative mating in relation to plumage traits shared by male and female American Robins. Condor 113:881–889

Shaner P-J, Chen Y-R, Li J-W, Kolbe JJ, Lin S-M (2013) Sex-specific correlations of individual heterozygosity, parasite load, and scalation asymmetry in a sexually dichromatic lizard. PLoS One 8:e56720

Sol D, Elie M, Marcoux M, Chrostovsky E, Porcher C, Lefebvre L (2005) Ecological mechanisms of resource polymorphism in Zenaida doves of Barbados. Ecology 86:2397–2407

Sommer S (2005) MHC-dependent mate choice in a monogamous rodent. Behav Ecol Sociobiol 58:181–189

Stutchbury BJM, Morton ES (2008) Recent advances in the behavioral ecology of tropical birds. Wilson J Ornithol 120:26–37

Svensson E, Nilsson JA (1997) The trade-off between moult and parental care: a sexual conflict in the blue tit? Behav Ecol 8:92–98

Szulkin M, Bierne N, David P (2010) Heterozygosity-fitness correlations: a time for reappraisal. Evolution 64:1202–1217

Thünken T, Meuthen D, Bakker TCM, Baldauf SA (2012) A sex-specific trade-off between mating preferences for genetic compatibility and body size in a cichlid fish with mutual mate choice. Proc R Soc Lond B 279:2959–2964

Tidemann SC, Woinarski JCZ (1994) Moult characteristics and breeding seasons of Gouldian *Erythrura gouldiae*. Masked Poephila personata and Long-tailed Finches P. acuticauda in savannah woodland in the Northern Territory. Emu 94:46–52

Tomiuk J, Stauss M, Segelbacher G, Fietz J, Kömpf J, Bachmann L (2007) Female genetic heterogeneity affects the reproduction of great tits (*Parus major* L., 1758) in low-quality woodlands. J Zool Syst Evol Res 45:144–150

Tregenza T, Wedell N (2000) Genetic compatibility, mate choice and patterns of parentage. Mol Ecol 9:1013–1027

van Oosterhout C, Hutchinson WF, Wills DPM, Shirley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Wagner RH (1999) Sexual size dimorphism and assortative mating in razorbills (*Alca torda*). Auk 116:542–544

Weimerskirch H (1991) Sex-specific differences in moult strategy in relation to breeding in the wandering albatross. Condor 93:731–737

Wetzel DP, Stewart IRK, Westneat DF (2012) Heterozygosity predicts clutch and egg size but not plasticity in a house sparrow population with no evidence of inbreeding. Mol Ecol 21:406–420

Wiley JW (1991) Ecology and behavior of the Zenaida dove. Ornitol Neotrop 2:49–75

Wyndham E (1986) Length of birds' breeding seasons. Am Nat 128:155–164