

hosts (Zink 2000; Andersson 2001; Lopez-Sepulcre & Kokko 2002).

The mechanisms leading to potential kin-biased egg donation are still unknown (for discussion about potential mechanisms, see Andersson 2001; Semel & Sherman 2001; Lopez-Sepulcre & Kokko 2002; Pöysä 2004; Andersson & Waldeck 2007). Natal philopatry has been viewed as a null hypothesis, because it results in elevated local relatedness which, coupled with parasite preference for nearby hosts, may lead to kin-biased egg donation. This null hypothesis has, however, been refuted by recent empirical evidence which suggests that some mechanism of kin recognition is involved in kin-biased egg donation (Andersson & Åhlund 2000; Andersson & Waldeck 2007; Waldeck *et al.* 2008). Seen from an inclusive fitness perspective, the overall

microsatellite loci described in Jaari *et al.* (2009) and listed in Table A1, Supporting information. Polymerase chain reaction (PCR) amplifications were carried out in a total volume of 10 μ L (2 pmol of each primer, 1 \times QIAGEN Multiplex Master Mix, 0.5 \times Q-Solution, and *c.* 30 ng of DNA) using the same cycling profile (15 min at 95 $^{\circ}$ C, followed by 30 cycles of 30 s at 94 $^{\circ}$ C, 90 s at 56 $^{\circ}$ C and 60 s at 72 $^{\circ}$ C and a final extension for 10 min at 72 $^{\circ}$ C) for all markers, using a commercial multiplex PCR kit (QIAGEN). The PCR products were diluted 1:750 with MQ-water and mixed with Et-ROX 400 standard (GE Healthcare, Life Sciences) according to the manufacturer's instructions and were resolved in a MegaBACE 1000 capillary sequencer (GE Healthcare, Life Sciences). Genotypes were scored using Fragment Profiler 1.2 software (GE Healthcare, Life Sciences). More details about used primers, loci and their variability are given in the Table A1 and Jaari *et al.* (2009).

Detection of CBP

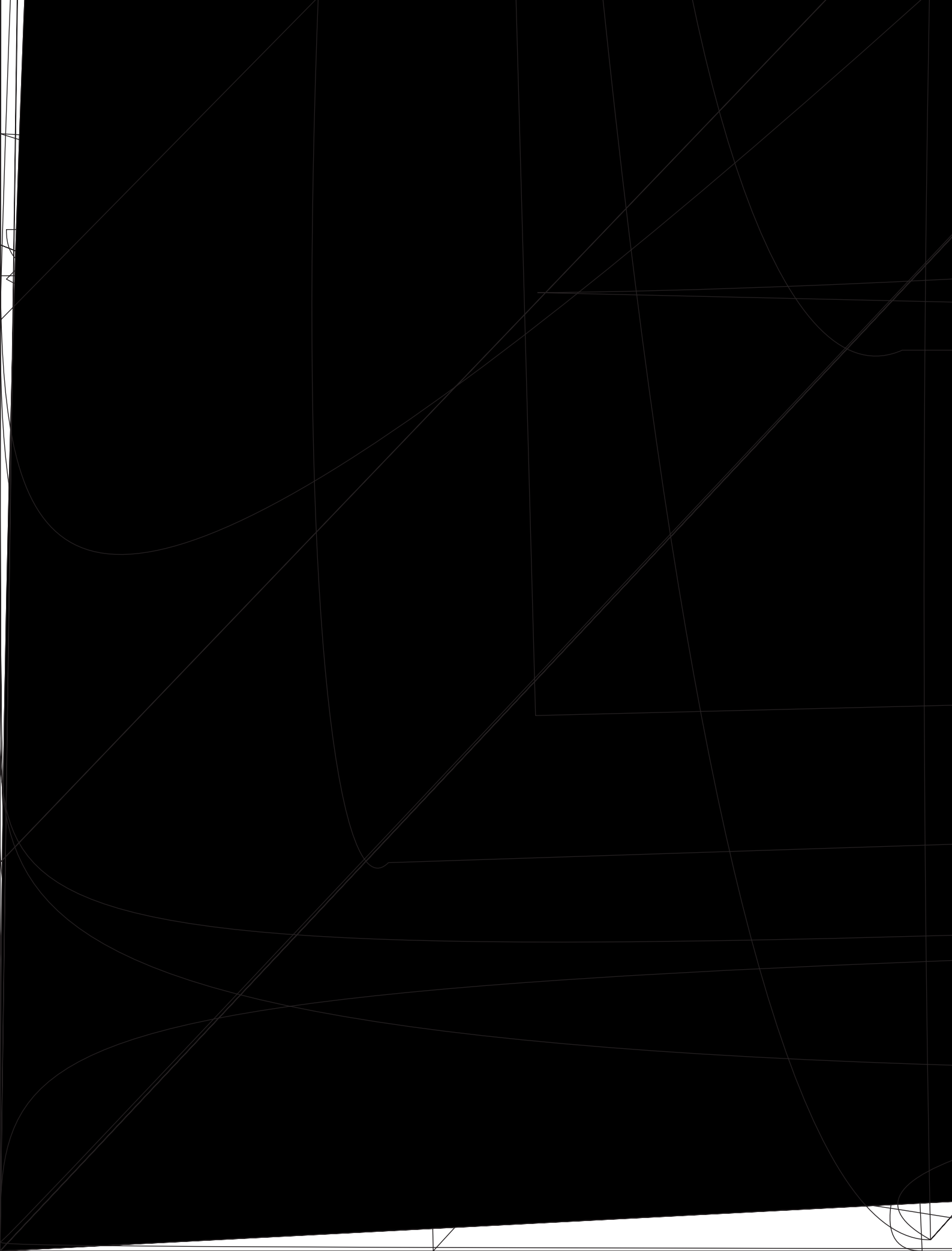
Loci were tested for deviations from Hardy–Weinberg equilibrium and linkage disequilibria using *FSTAT* 2.9.3.2 (Goudet 1995). Nonexclusion probabilities were calculated using Cervus 3.0 (Kalinowski *et al.* 2007). This statistic describes the average probability that the genotypic data will not exclude an unrelated candidate parent to be the parent – in this case mother – of an arbitrary offspring when the genotype of the other parent – in this case the father – is unknown.

Maternities were assigned to all the 288 sampled ducklings using the likelihood approach implemented in Cervus 3.0 (Kalinowski *et al.* 2007). Cervus estimates the likelihood ratios for each mother–offspring pair over all loci, given the genotypic data provided. Using the difference in likelihoods between the likeliest and second likeliest pair, Cervus can assign

neighbours and/or host–parasite pairs were on average more closely related than the rest of the population.

Parasitism behaviour

To examine the relative importance of relatedness and distance in determining the degree of parasitism by nesting parasites, we built a multinomial logistic regression model (McCullough & Nelder 1989), with relatedness and distance between nests being used to explain the probability that female i laid each egg in the nest of female j . The model is conditional on the total number of eggs laid by female i in a nest other than her own, and also on the nest of female j



of both relatedness and the number of parasitic eggs on the number of host eggs would be the opposite (positive) or indeed absent. Hosts did not donate eggs in response to parasitism, as there was no correlation between the number of parasitic eggs received and the number of eggs donated by the host ($r_p = -0.19$, $P > 0.3$, $n = 18$). The total number of young hatched in host nests was also uncorrelated with host–parasite relatedness ($r_p = -0.34$, $P > 0.16$, $n = 18$), and total clutch size was unrelated to the proportion of eggs hatching ($r_p = -0.17$, $P > 0.3$, $n = 29$). Details about clutch sizes in relation to parasitism status and the numbers of eggs donated are presented in Table 1.

Discussion

We found that host–parasite relatedness followed the pattern of spatial genetic structuring expected under natal philopatry (Waldeck *et al.* 2008), with both close neighbours and host–parasite pairs being more closely related to each other than to random females drawn from the population. However, we found that both distance and relatedness to potential hosts were associated with the number of eggs donated by nesting parasites, and that hosts appeared to reduce their clutch size as a response to parasitism. While host–parasite relatedness might be explained through more synchronous egg laying of related females, a condition facilitating parasitism (Sorenson 1993), this explanation is made less likely by our finding that the degree of host clutch reduction was positively related to host–parasite relatedness; a novel insight in the context of CBP research. Both the latter result and the finding of relatedness affecting the degree of parasitism suggest that hosts and parasites modify their behaviour in response not only to the behaviour of one another but also to their kinship to one another.

Spatial relatedness and parasite behaviour

Several studies have documented natal philopatry in female waterfowl (Anderson *et al.* 1992; Pöysä *et al.* 1997; Andersson & Åhlund 2000; Ruusila *et al.* 2000; Scribner *et al.* 2001; Andersson & Waldeck 2007; Waldeck *et al.* 2008), some of which have also found elevated relatedness between closely breeding females (McKinnon *et al.* 2006; Andersson & Waldeck 2007; Waldeck *et al.* 2008). It is thus important to assess whether the observed pattern of relatedness is the result of natal philopatry alone.

Our results show that both distance and relatedness *independently* affected the extent of parasitism by nesting parasites, so that the number of eggs donated increased with both decreasing distance and increasing relatedness. Hence, natal philopatry – although possibly present in

not mutually exclusive, processes. First, natal philopatry may be facilitating the proximity of relatives. Second, a closely related species, the common goldeneye (*Bucephala clangula*), has been documented to prioritize safe nest sites when parasitizing (Pöysä 1999). A closer examination of the fate of host nests includ

donors, as well as elucidating whether negotiation between hosts and parasites occurs.

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