

were scan sampled (Altmann 1974) every 45 seconds. Feeding and resting were the dominant activities (Table 1). Feeding activity was relatively low, however, compared to observations during winter in central Wales (Fox 1994).

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## Inbreeding in a Black Woodpecker *Dryocopus martius* population

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Although relatively rare in wild populations of birds, inbreeding has been observed in several species (see review by Ralls et al. 1986). Whether matings between kin occur less frequently in dispersed nesters than expected under the assumption of random pairing is difficult to assess, but in two studies of the Great Tit *Parus major*, no difference was apparent, given the dispersal pattern in the populations (Greenwood et al. 1978, Tienderen & Noordwijk 1988). So in the Great Tit – and apparently in many other species – mechanisms of inbreeding avoidance appears to be absent or, at best, imperfect. This would be expected if inbreeding had no marked effect on individual fitness (at the population level, inbreeding may often be unimportant (e.g. Lande 1991)). However, negative effects of inbreeding were apparent in the Great Tit in Whytham Wood, Britain (Greenwood et al. 1978) and in Vlieland, the Netherlands (Noordwijk & Scharloo 1981, Noordwijk & Balen 1988), and inbreeding depression seems to have hastened the extinction of the remnant population of Middle Spotted Woodpecker *Dendrocopos medius* in Sweden (Petersson 1985).

The present paper reports on the occurrence of inbreeding in a small Black Woodpecker *Dryocopus martius* population, including the kind of relationship between pair mates.

#### Material

In a 4700 km<sup>2</sup> study area spanning the border between Denmark and Germany almost all Black Woodpecker

broods (117, totalling 327 nestlings) have been ringed since 1982, and 164 full-grown birds (68 formerly ringed as nestlings) have been caught and colour-ringed (Christensen 2002). As a result, already by 1984 most of the breeding birds were individually recognizable, and in less than 10 of the pairs present since 1982 were one or both mates not identified. By the end of 2002, there had been 72 pair combinations of known birds, of which 11 pairs were still together. Of a total of 149 breeding cases (pair-seasons with one or more breeding attempts) these 72 pairs accounted for 140.

#### Results

Each year since 1989, the members of one or more of the pairs have been known to be related, giving a total of 10 "related pairs" of which two were still together by the end of 2002. For the remaining 62 pairs ("unrelated pairs") no knowledge of a kinship between the mates existed because these birds had been ringed as full-grown, or because their known pedigree did not go back far enough in time. So, although the members of some "unrelated pairs" may in fact have been related to some extent, the average degree of kinship was probably much less than in the "related pairs". The related pairs accounted for 27 breeding cases, the unrelated pairs for 113. Further information on the related pairs is given in Table 1, and pedigrees of the pair members are shown in Fig. 1.

On average, the related pairs produced fewer young per breeding season (1.59) than the unrelated pairs (2.39, excluding two pairs each producing an unknown number

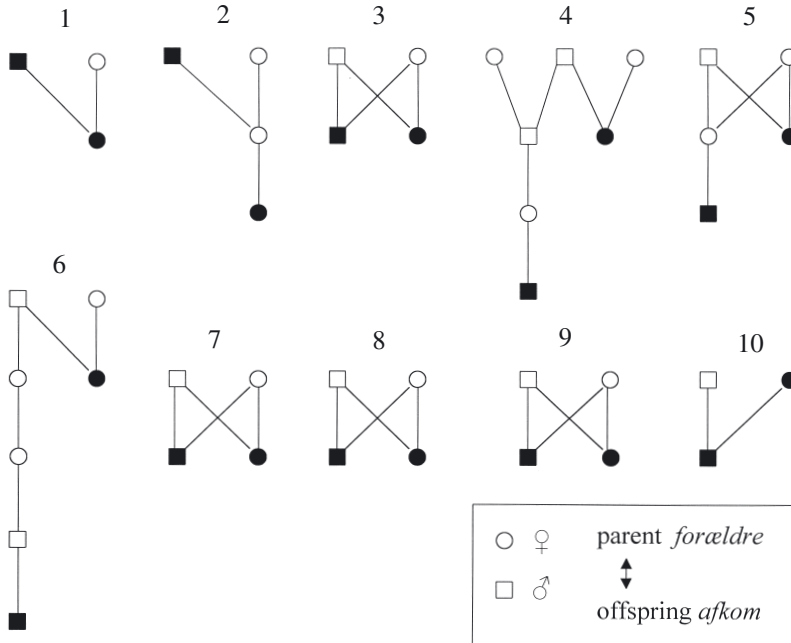


Fig. 1. Pedigrees for pair members of related pairs (the lowermost male and female in each graph, shown as filled symbols). The pairs thus consisted of father-daughter (1), grandfather-granddaughter (2), full siblings (3), etc. The siblings in pair 3, 8 and 9 were from different broods (seasons), in pair 7 from the same brood. The male in pairs 1 and 2 was the same, as were the male in pairs 7 and 8, and the female in pairs 3 and 4. The male in pair 6 was inbred (offspring from pair 4).

*Slægtskab mellem magerne i de ti beslægtede par. Parrets mager var i hvert tilfælde den nederste han og hun i diagrammet (sorte symboler) – altså far-datter (1), morfar-datterdatter (2), helsøskende (3), osv. I par 3, 8 og 9 var der tale om søskende fra forskellige kuld (år), i par 7 fra samme kuld. Hannen i par 1 og 2 var den samme, ligeledes hannen i par 7 og 8, og hunnen i par 3 og 4. Hannen i par 6 var selv indavlet (unge af par 4).*

Table 1. Data on the ten related pairs of Black Woodpecker.  
*Data for de ti beslægtede sortspættepar.*

Pair	F <sup>a</sup>	Breeding	Failed clutches	Relaid clutches	Failed/Total seasons	Total chicks	Chicks/season
Par		Yngleår	Mislykkede kuld	Omlæg	Mislykkede/alle sæsoner	Unger i alt	Unger/sæson
1 <sup>b</sup>	1/4	1989-1993	1	1	0/5	13	2.6
2 <sup>b</sup>	1/8	1994-1996	1	1	0/3	6	2.0
3 <sup>b</sup>	1/4	1989-1991	2	1	1/3	2	0.7
4 <sup>b</sup>	1/32	1992-1997	3	0	3/6	6	1.0
5	1/8	1995-1996	1	0	1/2	3	1.5
6	1/64	1996	1	0	1/1	0	0
7	1/4	1998-2000	1	0	1/3	5	1.7
8 <sup>c</sup>	1/4	2001-2002	1	1	0/2	5	2.5
9	1/4	1999	1	0	1/1	0	0
10 <sup>c</sup>	1/4	2002	0	0	0/1	3	3
All	0.180	1989-2002	12	4	8/27	43	1.6

<sup>a</sup> Coefficient of kinship (e.g., Crow & Kimura 1970) *Indavlskoefficient*

<sup>b</sup> Also included in Christensen (1995) *Også nævnt i Christensen (1995)*

<sup>c</sup> Pair still together at end of study *Parret stadig intakt ved undersøgelsens afslutning*



of young during a single season). However, when using the mean production of young per season for the pairs as the observations and comparing the related ( $n=10$ ) and unrelated ( $n=60$ ) pairs, the result was not quite significant statistically (Mann-Whitney U-test,  $P=0.08$ ). To a large extent this was caused by the fact that a larger proportion of unrelated (34) than of related (3) pairs stayed together for one breeding season only, and such pairs produced relatively few young. If the test was repeated while disregarding the first season for all pairs, the difference between related (1.65;  $n=7$ ) and unrelated (2.84;  $n=26$ ) pairs was strongly significant (Mann-Whitney U-test,  $P=0.009$ ).

Since some individual woodpeckers participated in more than one pair combination, pairs are not strictly independent units and the tests are at best approximate. Nevertheless, our results do suggest the presence of some negative effect on the survival of inbred eggs or nestlings in this woodpecker population.

### Discussion

That inbreeding depression is a real phenomenon, not only in captive animals but also in natural populations, seems beyond doubt. That it has rarely been shown in natural populations appears primarily to be due to the difficulties in obtaining adequate data. In the present case of the Black Woodpecker our results were strongly suggestive of inbreeding depression, although not entirely conclusive. They might have been more convincing if a negative relationship between the degree of kinship between pair members and their breeding success had

been apparent, but our sample was too small to show such a relationship which is likely to exist in a general or statistical sense, but hardly for individual pairs.

Granted the existence of inbreeding depression, the presence of mechanisms of avoiding inbreeding could be expected. Sex-biased natal and breeding dispersal is often viewed as such a mechanism, although other benefits of dispersal are possible and – at least in some cases – appear more important than inbreeding avoidance (Ralls et al. 1986, and references therein). In our Black Woodpecker population, female-biased natal dispersal was suggested but not very marked (Christensen 2002). However, when kin of different sex do meet after dispersal, they may not recognize each other. Kin recognition often seems to be based on familiarity which generally wanes after a period of separation (Ralls et al. 1986), and chance pairing of kin may usually be too rare to exert a significant selection pressure towards extending memory in this respect. In small populations chance pairings between kin will be more common (present study; cf. also the Middle Spotted Woodpecker and the White-backed Woodpecker *Dendrocopos leucotos* in Sweden (Pettersson 1985, Aulén & Carlson 1990), among other cases); but in small populations, inbreeding may actually be the best option, if the alternative is to postpone breeding indefinitely.

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### Resumé: Indavl blandt Sortspætter i det dansk-tyske grænseland

I den lille bestand af farveringmærkede Sortspætter *Dryocopus martius* i det dansk-tyske grænseland (se Christensen 2002) har der i perioden 1982-2002 været 10 par, hvor magerne var beslægtede i forskellig grad (Fig. 1 og Tabel 1). I samme periode var der 62 "ubeslægtede" par, dvs. farvemærkede par, hvor der intet kendskab er til et evt. slægtskab, enten fordi en eller begge fugle er blevet mærket som voksne, eller fordi kendskabet til deres stamtræ ikke går tilstrækkeligt langt tilbage i tiden. Magerne i de "ubeslægtede" par kan derfor godt være mere eller mindre beslægtede, men givetvis i gennemsnit i meget mindre grad end i de 10 "beslægtede" par.

I perioden var der i alt 140 yngletilfælde (par-sæsoner med et eller flere yngleforsøg); 27 blandt de beslægtede par, 113 blandt de ubeslægtede par. Normalt anses indavl for skadeligt i og med, at det øger graden af homozygositet hos afkommet, hvilket i reglen mindsker deres "fitness". Det kan give sig udslag i nedsat levedygtighed og/eller frugtbarhed hos afkommet. Regnet pr sæson producerede de beslægtede par da også færre unger end de ubeslægtede (1,59 vs 2,39), men forskellen var ikke signifikant. Imidlertid var der flere par blandt de beslægtede end blandt de ubeslægtede, der kun var sammen i én sæson, og generelt producerede spætteparrene få unger i deres første sæson. Testen blev derfor gentaget med udelukkelse af parrenes første sæson (hvorved antallet af indgående par reduceredes til 7 og 26 for hhv. beslægtede og ubeslægtede par); herved steg ungeproduktionen hos de to grupper til hhv. 1,65 og 2,84 pr sæson, og forskellen var stærkt signifikant (Mann-Whitney U-test,  $P=0,009$ ).

Parrene var dog ikke strengt uafhængige enheder, da nogle Sortspætter indgik i flere parkombinationer, så testen er kun en tilnærmelse. Men den antyder i det mindste eksistensen af en mærkbar indavlsdepression i denne bestand. Mere utvetydige konklusioner i samme retning er gjort for Musvitter *Parus major* i såvel England som Holland, men generelt er undersøgelser af spørgsmålet sjældne, især når det gælder spredt-rugende territoriale arter, da det er svært at tilvejebringe et egnet materiale.

Hvis indavl nedsætter fitness, burde der selekteres for mekanismer, der modvirker det. Spredning, især når ét køn tenderer til at flytte over større afstande end det andet, anses normalt for en sådan mekanisme. Men når beslægtede fugle siden alligevel mødes, er det nok et stort spørgsmål, om de genkender hinanden. Fugle, der lever i grupper (incl. par og forældre/unger), kan tydeligvis genkende hinanden, men denne evne falder med tiden, når de ikke længere færdes i samme område og mødes. I normale bestande er indavl gennemsnitligt et ubetydeligt problem, så der er ikke vundet meget ved at forlænge hukommelsen på det punkt. I små bestande er risikoen for tilfældige pardannelser mellem beslægtede

fugle større; men her kan indavl samtidig være at foretrække, da alternativet vil være at udsætte ynglen på ubestemt tid.

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