Alloparental behaviour in Mute Swans *Cygnus olor* detected by DNA fingerprinting

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A pair of Mute Swans was located on the River Ivel in England that were accompanied by an unusually large number of cygnets. The application of DNA fingerprinting to blood samples taken from the birds revealed that the cygnets comprised two sets of cygnets. Nine cygnets were the genuine progeny of the attendant adults. The other six were full siblings among themselves, and were related less closely to the remainder. It is suggested that six cygnets were adopted from an adjacent family, one of whose parents was probably related to the adopting male.

Many studies of swans involve the observation of flocks on the wintering grounds, and the identification of family parties from behavioural data. These 'families' usually consist of two adults with one or more accompanying juveniles that may be up to a year old. There is, however, no way of determining from observational data whether the birds involved really are related to one another: extra-pair fertilization, egg-dumping and adoption have all been recorded in other species, and the last of these has been reported in Mute Swans (Bacon 1980).

We have recently reported the existence of extensive variation in polymorphic minisatellite in Mute, Whooper and Bewick's Swans, *Cygnus olor, C. cygnus* and *C.bewickii*, and showed that these 'genetic fingerprints' are sufficiently variable to permit the unique recognition of individual birds within a population (Meng *et al.* 1990). Here we show that this variation is also sufficient to determine parentage within a 'family' of Mute Swans that consisted of an unusually large number of cygnets.

Mute Swans regularly nest on the River Ivel in Bedfordshire, England. In early May 1988, a lady observed a pair of swans (Pair A) with nine cygnets. They had nested on the bank of the river at a site used regularly for several years. A second pair of swans (Pair B) had nested on an island in an adjacent lake. These two adults remained on the lake but were never seen with any cygnet. The day after she saw pair A with nine cygnets, the lady saw two adults with 15 cygnets on the river. Thereafter she never saw less than 15 until 16 July when the complete 'family' of 17 swans were trapped. The adults on the adjacent lake were not captured.

Methods

Blood samples of about 1 ml were taken from the tarsal vein of each swan, and stored at -20°C until analysis. DNA was extracted using the method described by Wetton *et al.* (1987). Approximately 4µg of DNA was digested with Hae III and subjected to electrophoresis through 0.8% agarose gels 20cm long. Electrophoresis was stopped when fragments less than 2Kb in size had migrated off the end. Transfer of DNA to Amersham HYBOND-N nylon membrane, and prehybridization were performed as described by Wetton *et al.* (1987). Hybridization was undertaken using the RNA probes pSPT 19.6 and 19.15, subcloned from human minisatellite probes 33.6 and 33.15 (Carter *et al.* 1989). Hybridization, wash and autoradiography followed Meng *et al.* (1990).

Results

A blot containing the DNA of the two adults and 15 cygnets was hybridized with human minisatellite probe 19.15, and individual specific fingerprints were obtained (Fig. 1). There is an average of 20.8 bands per cygnet in these fingerprints (Table 1A), and all of the bands revealed in cygnets A, C, D, F, G (except two), J, L, N and O are present in one or other of the parents. Many studies of the inheritance of DNA fingerprints have shown that, apart from occasional mutations, each band present in an offspring can be traced back to the parents. The mutation rates have been estimated at about 1 in

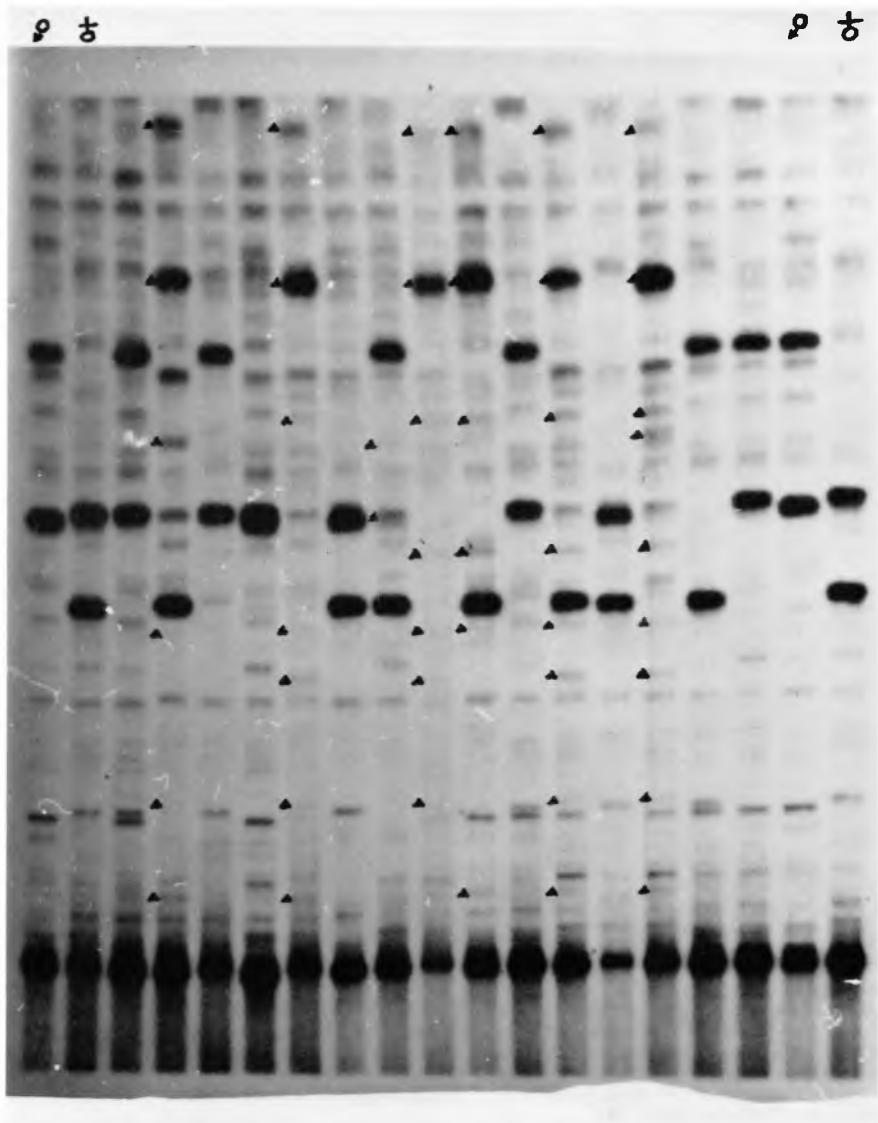

Figure 1 DNA fingerprints of the Mute Swan adults and accompanying cygnets. DNA preparations of all the individuals were fingerprinted with probe pSPT 18.15. Bands present in cygnets, which are absent in both adults, were marked "▼" and referred to as novel bands. Cygnets B, E, H, I, K and M, which have many novel bands, are mismatched cygnets. , male adult; , female adult.

200 in a variety of species (Jeffreys *et al.* 1985). Cygnets B, E, H, I, K and M possess from 6 - 9 novel bands, and it seems very unlikely that they have arisen as the result of mutation. Rather, we conclude that these six cygnets are unrelated to one or both of the adults that are attending them.

To confirm this conclusion, the DNA samples were re-analysed using a second human minisatellite probe (Figs. 2a and 2b). The cygnets show an average of 22.0 bands in the resulting fingerprints (Table 2a). The same six cygnets possess bands that are absent from the adults: the remaining nine show close agreement apart from a couple of possibly mutant bands marked in Fig. 2b.

Parentage of these cygnets can be analysed using a modification of the methodology of Brookfield (1989) as used by Brookfield *et al.* (in

TABLE 1a The analysis of the DNA fingerprint patterns generated for 15 Mute Swan cygnets using probe pSPT 19.15. The number of bands that each cygnet shares with the attendant adult is shown

Progeny bands shared with	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	AV(SD)
Female	12	4	4	13	5	6	6	5	5	12	6	4	5	11	11	$7.3_{(3.41)}$
Male	6	5	7	8	7	8	8	5	6	5	8	7	7	5	4	$6.5_{(1.30)}$
Both	7	4	5	7	4	5	7	4	3	7	5	6	5	7	7	$5.6_{(1.30)}$
Neither	0	5	0	0	7	0	2	7	6	0	8	0	9	0	0	
TOTAL	25	18	16	28	23	19	23	21	20	24	27	17	26	23	22	$20.8_{(6.11)}$

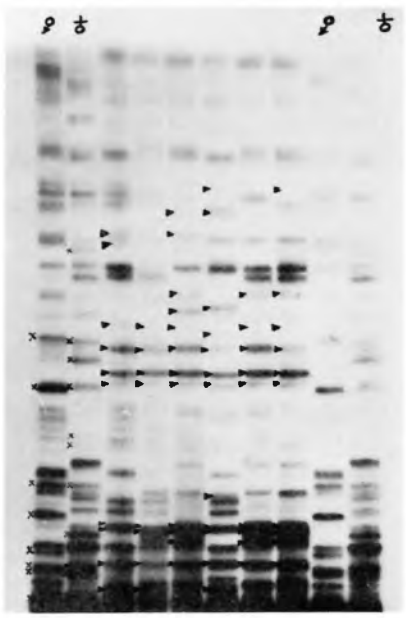

Figure 2a DNA fingerprints of the Mute Swan adults and mismatched cygnets. DNA digests were hybridised with probe pSPT 19.6. Adult DNA digests were loaded into slots at both ends. Bands present in the adults, which appear in none of the cygnets, were indicated as "X", while novel bands present in the cygnets are marked "▲"

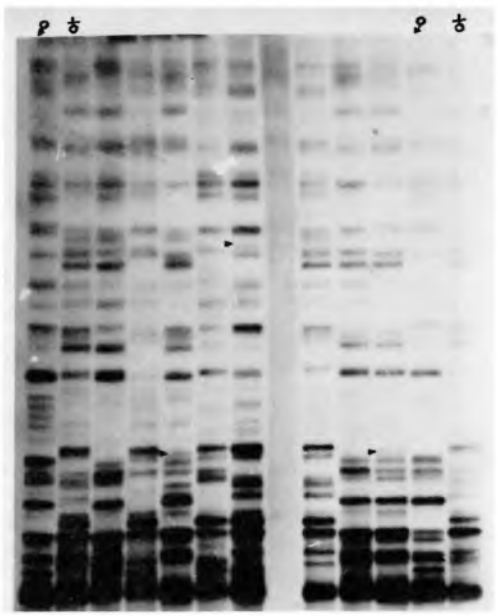

Figure 2b DNA fingerprints of the Mute Swan adults and their true brood. DNA fingerprints also resulted from hybridisation of DNA Hae III digests with probe pSPT 19.6. Adult DNA digests were loaded into slots at both ends. Mutation bands present in the offspring are marked "▲". DNA sample of cygnet J was degraded.

TABLE 2a The analysis of the DNA fingerprint patterns generated for 15 Mute Swan cygnets using probe pSPT 19.15. The number of bands that each cygnet shares with the attendant adult is shown.

Progeny bands shared with	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	AV(SD)
Female	8	5	9	10	5	8	11	1	4	13	3	9	7	8	5	$7.9_{(3.39)}$
Male	11	8	8	9	8	9	9	6	8	10	6	9	5	10	4	$8.2_{(1.81)}$
Both	5	4	4	5	1	4	3	3	2	3	2	5	1	6	3	$3.1_{(1.46)}$
Neither	0	9	0	1	8	0	1	12	12	0	9	0	10	1	0	
TOTAL	24	26	21	25	22	21	24	22	26	26	20	23	23	25	12	$22.0_{(6.34)}$

(a) excluded from means because poor track and fewer scorable bands

Table 1b. The probability of acquiring the fingerprint of each progeny from the two adults under four different models (see text for details). The results relate to the data in Table 1a. A plus indicates the most likely results: an asterisk indicates a result that is more than 100-times less likely.

	MOD 1	MOD 2	MOD 3	MOD 4
A	+ 1.5×10^{-9}	* 3.5×10^{-18}	* 1.4×10^{-13}	* 7.2×10^{-20}
B	* 3.6×10^{-24}	+ 3.5×10^{-17}	9.1×10^{-19}	9.0×10^{-18}
C	+ 2.3×10^{-11}	3.1×10^{-13}	* 1.4×10^{-16}	* 3.6×10^{-17}
D	+ 2.8×10^{-9}	* 2.4×10^{-18}	1.3×10^{-14}	* 9.1×10^{-21}
E	* 1.0×10^{-27}	+ 1.2×10^{-18}	* 4.1×10^{-21}	2.9×10^{-19}
F	+ 4.3×10^{-11}	* 2.7×10^{-14}	* 9.2×10^{-17}	* 4.5×10^{-18}
G	+ 1.0×10^{-14}	4.1×10^{-15}	* 1.4×10^{-17}	* 2.9×10^{-19}
H	* 6.8×10^{-29}	+ 4.0×10^{-19}	* 8.0×10^{-20}	1.1×10^{-19}
I	* 5.3×10^{-27}	1.8×10^{-18}	4.6×10^{-20}	+ 2.3×10^{-18}
J	+ 1.2×10^{-9}	* 2.0×10^{-18}	* 6.4×10^{-13}	* 1.4×10^{-19}
K	* 2.4×10^{-30}	+ 1.8×10^{-19}	* 6.1×10^{-22}	1.8×10^{-20}
L	+ 9.1×10^{-11}	5.3×10^{-13}	* 2.3×10^{-16}	* 1.8×10^{-17}
M	* 6.1×10^{-33}	+ 1.0×10^{-19}	* 3.6×10^{-22}	3.6×10^{-20}
N	+ 1.0×10^{-10}	* 9.0×10^{-18}	* 3.7×10^{-13}	* 2.9×10^{-19}
O	+ 8.1×10^{-10}	* 5.2×10^{-18}	* 1.6×10^{-12}	* 5.7×10^{-19}

prep.). The essentials of this are that the fingerprint pattern of each cygnet is compared with the adults under four hypotheses: (1) both adults are the parents; (2) the male is the father but the female is not the mother; (3) the female is the mother but the male is not the father; (4) neither adult is a parent. The probability of acquiring the trio of fingerprints under all four models is determined and the most likely model is recorded. The likelihood of this result can then be compared with the others to determine the relative probabilities. The method assumes the fingerprint bands are unlinked and therefore independent. Although we know that this is not entirely true (Meng *et al.* 1990), the effects of linkage do not materially affect our conclusions.

We have completed the calculations for the data generated with both probes, and show the results in Tables 1b and 2b. Band-sharing between the two adults is about 25.0% for probe 19.6 and 33.4% for 19.15. These are very close to the values derived for a more extended series of unrelated Mute Swans (Meng *et al.* 1990 and unpublished data), and we are fairly confident that the two adults are indeed unrelated. We will describe the results with probe 19.15 in some detail, including the other set for comparison at the end.

Table 1b shows the probability of obtaining the trio of fingerprints observed for the two adults and each progeny in turn. It is assumed that bands are inherited in a Mendelian fashion (see later) and that there is a certain level of mutation (0.005). The probabilities are calculated under each of the four models listed above. Individually, these probabilities are very small, for there are many millions of possible segregations of parental bands in a single progeny individual. However, the listed values re-

Table 2b. The probability of acquiring the fingerprint of each progeny from the two adults under four different models (see text for details). The results relate to the data in Table 1a. A plus indicates the most likely results: an asterisk indicates a result that is more than 100-times less likely

	MOD 1	MOD 2	MOD 3	MOD 4
A	+ 2.1×10^{-15}	* 1.9×10^{-19}	* 4.6×10^{-23}	* 3.6×10^{-24}
B	* 2.1×10^{-39}	+ 5.3×10^{-25}	* 1.3×10^{-28}	4.0×10^{-25}
C	+ 4.3×10^{-16}	* 6.0×10^{-21}	* 1.2×10^{-20}	* 9.6×10^{-23}
D	+ 5.8×10^{-18}	* 3.2×10^{-22}	* 6.6×10^{-21}	* 1.2×10^{-24}
E	* 1.6×10^{-38}	1.0×10^{-23}	* 2.6×10^{-28}	+ 3.2×10^{-23}
F	+ 4.3×10^{-16}	* 5.8×10^{-20}	* 1.3×10^{-21}	* 9.6×10^{-23}
G	+ 5.1×10^{-19}	* 2.2×10^{-23}	* 4.4×10^{-22}	* 3.6×10^{-24}
H	* 5.1×10^{-48}	1.0×10^{-24}	* 2.7×10^{-30}	+ 3.2×10^{-23}
I	* 2.9×10^{-48}	5.8×10^{-27}	* 1.5×10^{-31}	+ 4.0×10^{-25}
J	+ 2.8×10^{-16}	* 5.1×10^{-24}	* 9.8×10^{-22}	* 4.0×10^{-25}
K	* 9.0×10^{-41}	4.5×10^{-24}	* 1.1×10^{-27}	+ 2.9×10^{-22}
L	+ 1.8×10^{-14}	* 1.3×10^{-20}	* 2.9×10^{-21}	* 1.1×10^{-23}
M	* 1.0×10^{-43}	* 1.8×10^{-28}	* 3.6×10^{-27}	+ 1.1×10^{-23}
N	+ 1.8×10^{-16}	* 2.9×10^{-20}	* 6.9×10^{-23}	* 1.2×10^{-24}
O	+ 3.8×10^{-6}	* 9.0×10^{-11}	* 8.4×10^{-9}	* 3.4×10^{-12}

Table 3. The most likely familial relationship of each Mute Swan progeny to the two attendant adults. Where more than one relationship is listed, these cannot formally be separated.
B = both adults are parents
M = male is parent, female is not
F = female is parent, male is not
N = neither adult is a parent

	19.15	19.6
A	B	B
B	MFN	MN
C	BM	B
D	B	B
E	MN	NM
F	B	B
G	BM	B
H	MN	NM
I	NMF	NM
J	B	B
K	MN	NM
L	B	B
M	MN	N
N	B	B
O	B	B

late to the patterns actually observed under each model, and show some results that are quite clear cut.

For example, for progeny A, the most likely result is that arising from Model 1: the two adults are indeed its parents. The probabilities under the other three models are more than 100-times less likely, and can safely be discarded. For progeny B, the result is less clear: the most likely result occurs with Model 2 (the male is the father, but the female is not the mother). Model 1 is very much less likely. However, we cannot safely discard Models 3 and 4 since their probabilities are close to that under 2. Thus, we conclude that any of these three models is possible.

We can proceed in similar fashion through all of the progeny. For each, there is a 'most likely' model, and we can discard those models that differ from this by more than 100 times. The remaining 'non-separable' models are listed in Table 3 for both probes. Some progeny are unequivocal: A, D, F, J, L, N and O are clearly the offspring of the two trapped adults. The remainder are less clear-cut: a total of 8. We can obtain a 'pooled probability' for these by combining the individual values generated from each probe, and this suggests (Table 4) that C and G are also genuine progeny, but that M is the progeny of neither. The remainder (B, E, H, I, K) cannot be resolved. Each of them could equally

Table 4. Combined probability using both probes for those individuals that showed two or more non-separable models in Table 3.
B = both adults are parents
M = male is parent, female is not
F = female is parent, male is not
N = neither adult is a parent
A plus indicates the most likely model, an asterisk an alternative model whose probability is 100-times less likely.

PROG	MODEL	.16	.5	BOTH	Most likely
	M	3.5×10^{-17}	5.3×10^{-25}	1.9×10^{-41}	+
B	F	9.1×10^{-19}	1.3×10^{-28}	1.2×10^{-46}	*
	N	9.0×10^{-18}	4.0×10^{-25}	3.6×10^{-42}	
C	B	2.3×10^{-11}	4.3×10^{-16}	9.9×10^{-27}	+
	M	3.1×10^{-13}	6.0×20^{-21}	1.9×10^{-33}	*
E	M	1.2×10^{-18}	1.0×10^{-23}	1.2×10^{-41}	+
	N	2.9×10^{-19}	3.2×10^{-23}	9.3×10^{-42}	
G	B	1.0×10^{-14}	5.1×10^{-19}	5.1×10^{-33}	+
	M	4.1×10^{-15}	2.2×10^{-23}	3.1×10^{-38}	*
H	M	4.0×10^{-19}	1.0×10^{-24}	4.0×10^{-43}	
	N	1.1×10^{-19}	3.2×10^{-23}	3.5×10^{-42}	+
	M	1.8×10^{-18}	5.8×10^{-27}	1.0×10^{-44}	
I	F	4.6×10^{-20}	1.5×10^{-31}	6.9×10^{-51}	*
	N	2.3×10^{-18}	4.0×10^{-25}	9.4×10^{-43}	+
K	M	1.8×10^{-19}	4.5×10^{-24}	8.1×10^{-43}	
	N	1.8×10^{-20}	2.9×10^{-22}	5.2×10^{-42}	+
M	M	1.0×10^{-19}	1.8×10^{-28}	1.8×10^{-47}	*
	N	3.6×10^{-20}	1.1×10^{-23}	4.0×10^{-43}	+

Table 5. The results of comparing all 15 Mute Swan progeny in pairs using probes pSPT 19.5(A) and 19.6(B). The most likely relationship is shown for each comparison: F = full sibling, H = half-sibling, U = unrelated individuals.

A

	K	I	H	E	B	M	O	N	L	J	G	F	D	C
A	H	H	H	H	H	H	F	F	F	F	F	F	F	F
C	H	H	F	F	F	H	F	F	F	F	F	F	F	
D	F	H	H	F	H	F	F	F	F	F	F	F		
F	F	F	H	H	F	H	F	F	F	F	F			
G	F	H	H	F	F	F	F	F	F	F				
J	H	H	H	H	H	H	F	F	F					
L	F	F	H	F	F	H	F	F						
N	F	H	F	H	H	H	F							
O	F	H	F	F	F	F								
M	F	F	F	F	F									
B	F	F	F	F										
E	F	F	F											
H	F	F												
I	F													

B

	K	I	H	E	B	M	O	N	L	J	G	F	D	C
A	H	U	H	H	H	U	F	F	F	F	H	F	F	F
C	H	U	H	H	H	H	F	F	F	F	F	F	F	
D	H	U	U	H	H	U	F	F	F	F	H	H		
F	H	U	H	U	H	H	H	H	F	F	F			
G	H	H	H	H	H	U	U	H	H	F				
J	H	H	H	H	H	H	F	F	F					
L	H	U	H	H	H	H	H	F						
N	H	U	H	H	H	H	F							
O	U	U	U	U	U	U								
M	F	F	F	F	F									
B	F	F	F	F										
E	F	F	F											
H	F	F												
I	F													

be the progeny of the male alone, or neither.

We can now approach the problem from another direction. Just as it is possible to compare adult and progeny fingerprints to determine the probability that they are related, so it is possible to screen progeny in pairs to assess the probability of their being siblings (Brookfield *et al.* in prep). We have done this with all the progeny data. This analysis is less sensitive, so many of the results are not significant. Nevertheless, when we simply list the most likely relationship between all possible pairs using each probe (Table 5), some consistent patterns emerge. The family results described above suggested that A, C, D, F, G, J, L, N and O are the genuine progeny of the adults that accompanied them. The sibling analysis using probe 19.15 confirms this, for it reveals patterns to be expected if all of these cygnets were full siblings. Similarly, it suggests that M, B, E, H and I are also full siblings. These conclusions are supported by the data from probe 19.6.

Comparing these two groups of siblings, there is no doubt that they are more similar to each other than we would expect were they unrelated. The actual degree of relationship is, however, not clear, although over 50% of the comparisons suggest they are sets of half-siblings.

Analysis of the inheritance of heterozygous parental bands also excludes the probability that all of the 15 cygnets belong to the same family. When using probe pSPT 19.15, the number of cygnets inheriting each heterozygous parental band did not follow the expected binomial distribution, while it did follow the law after excluding the mismatched cygnets from the family (data not shown). In the DNA fingerprints of mismatched cygnets detected with probe pSPT 19.6, 15 heterozygous maternal bands are transmitted on average to 31.1% of mismatched cygnets and 18 heterozygous paternal bands shown 24.1% transmission. The

segregation of parental bands deviates from the expected Mendelian inheritance largely due to many parental bands transmitted to none of the cygnets (Table 6). By contrast, the segregation of maternal bands or paternal bands among the nine offspring is strictly consistent with the expected binomial distribution.

Discussion

Courtship and mating behaviour are complex in avian species. Extra-pair copulations and fertilization (EPC and EPF - see review by Ford 1983), intra-specific nest parasitism (INP - review by Yom Tov 1980) and alloparental care (review by Riedman 1982) have all been observed, even among apparently monogamous species. Study of mating systems generally depends upon analysing the social relationship between the adults and the attendant young. However, the identification of unambiguous genetic kinship is crucial to many evolutionary theories of behavioural ecology. For example, the recent interest in Lifetime Reproductive Success (Newton 1989) must assume throughout that young are the biological offspring of the attendant adults, while recognizing that this may not be the case.

Yet it is this determination of kinship between adults and young that is so difficult in wild populations. Genetical markers in morphology have been used to assign parentage (Burns *et al.* 1980), and electrophoretic analysis of proteins has revealed multiple maternity and paternity within single broods of Eastern Bluebirds, *Sialis sialis* (Gowaty & Karlin 1984). Westneat (1987) also used polymorphic enzyme loci for parental exclusion in Indigo Buntings, *Passerina cyanea.* Restriction fragment length polymorphism (RFLPs) have been used to detect INPs and EPFs in single broods of the Lesser Snow Goose, *Chen caerulescens* (Quinn *et al.* 1987). However, such studies may often fail to recognise non-parentage because of low heterozygosity and insufficient loci.

We have shown here that DNA fingerprinting, first developed in man (Jeffreys *et al.* 1985), can simultaneously detect a number of minisatellites with multiple alleles in swans, and provides a new type of genetic marker for these species, paralleled by those for a wide range of other animals (Wetton *et al.* 1987; Burke & Bruford 1987). The present results suggest that of a party of 15 Mute Swan cygnets, six were not the progeny of the attendant pair of adults, although they were full siblings among themselves, and possibly half-siblings of the remaining nine cygnets. Observational data suggested that the mismatching cygnets had been acquired by the adults shortly after hatching.

Such alloparental care and the adoption of young has been documented in over 120 mam-

Table 6. Segregation analysis of heterozygous parental bands in the Mute Swan cygnets (from Fig. 2a and 2b)

Transmission to No. Cygnets	From Fig. 2a				From Fig. 2b			
	Male		Female		Male		Female	
	Exp[b]	Obs	Exp	Obs	Exp	Obs	Exp	Obs
0	0.28	8	0.2	4	0.07	0	0.08	0
1	1.69	1	1.41	4	0.59	0	0.66	1
2	4.22	3	3.52	2	2.08	3	2.30	2
3	5.63	5	4.69	1	4.16	5	4.60	5
4	4.22	1	3.52	3	5.20	6	5.74	10
5	1.69	0	1.41	1	4.16	5	4.60	1
6	0.28	0	0.23	0	2.08	0	2.30	2
7					0.59	0	0.66	0
8					0.07	0	0.08	0
Total		18		15		19		21
Statistic Test	$\chi^2 = 217.98$ (S)c		$\chi^2 = 70.55$ (S)		$\chi^2 = 7.09$ (N.S.)		$\chi^2 = 4.29$ (N.S.)	
Transmission frequency	24.07%		31.11%		46.05%		45.83%	
(S.E.M.)	(5.75%)		(7.43%)		(3.03%)		(3.27%)	

a. Heterozygous parental band: a band present in only one of adults and not transmitted to all the cygnets.
b. Obs., observed: Exp. expected values: expected binomial distributions
c. S = Significant at the level of 0.05. N.S. = Non-significant.

malian and 150 avian species (Riedman 1982). Among waterfowl, it is well known in Eider Ducks *Somateria mollisima* and Geese, *Anser* spp, and has also been recorded in Mute Swans (Bacon 1980). However, records directly referrable to adoption can only be obtained from well-known, ringed or web-tagged populations. Circumstantial observations, such as an unexpected increase in brood size can be informative. When these are paralleled by the equivalent decrease of an adjacent brood, the evidence becomes stronger. However, it is still necessary to use a technique such as DNA fingerprinting to confirm the relatedness of the birds involved.

The reasons why this particular adoptive behaviour took place are not clear. All the cygnets were identified at a very young age and adoption must have taken place within a couple of days of hatching. Cooperative behaviour of young birds commonly involves non-breeders, thus alloparenting might be of benefit for the experience of caring for young (Riedman 1982). Birkhead and Nettleship (1984) reported that alloparental behaviour was most common among failed breeders in the Common Guillemot, *Uria aalge*, but in the present case, the alloparents were neither non-breeders nor failed breeders. Bacon (1980) suggests two causes of adoption more particular to Mute Swans: territorial intrusion, where the intruding adults are driven off faster than their cygnets can follow, and cygnets getting washed over a weir (especially during floods) and 'acquired' by adults downstream. The former is the more likely of these two in the present study, for there was neither weir nor flood at the time. However, there is no direct evidence in its support.

The results suggest that the adopted cygnets were a group of siblings, and quite closely related to the true progeny - possibly even being half-siblings. Coleman & Minton (1980) showed that young Mute Swans (especially females) return to nest close to, or even on, their own natal territory. Furthermore, in the few recorded instances of bigamy, the second female is commonly a daughter of the bigamous male. Thus a possible explanation of the apparent close relationship between the two families is that the mother of the adopted brood was the daughter of male of Pair A. This could account for the similarity between the adopted brood and the attendant male. It is, therefore, particularly unfortunate that pair B could not be trapped for sampling and analysis.

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