MONOGAMY IN LEACH'S STORM-PETREL: DNA-FINGERPRINTING EVIDENCE

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ABSTRACT.—We used multilocus minisatellite DNA fingerprinting to estimate the frequency of extrapair fertilizations in a population of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) on Kent Island, New Brunswick, Canada. Leach's Storm-Petrel is a member of Procellariiformes, an order of long-lived pelagic birds characterized by long-term pairbonds, single-egg clutches, and extended periods of parental care. We found no evidence of extrapair fertilizations in 48 families (42 full families and 6 partial families consisting of the putative father and the single offspring). Thus, our results indicate that the breeding system (genetic monogamy) matches the mating system (social monogamy) in our study population, a condition that no longer can be assumed in socially monogamous bird species. Genetic monogamy in Leach's Storm-Petrels may be maintained by last-sperm precedence and frequent copulation by mates during the female's fertile period. Such tactics employed by a male may yield a high probability of fertilizing the single egg laid by his mate. *Received 15 June 1994, accepted 31 August 1994.*

IN MOST AVIAN species, a male and a female form a pair bond and cooperate to produce offspring (Lack 1968). Trivers (1972), however, argued that socially monogamous males should be expected to pursue a strategy that maximizes the trade-off between parental effort and mating effort outside the pair bond. As the benefit of male parental care decreases, the cost of parental neglect lessens and the net benefit to males pursuing extrapair fertilizations (EPFs) increases. Females should be expected to seek EPFs, which may favor the acquisition of better genes for their offspring, increase genetic diversity among offspring, increase the probability of fertilization, or yield other material benefits through courtship feeding or increased parental care (reviewed by Westneat et al. 1990, Birkhead and Møller 1992). Thus, there are potential fitness gains associated with extrapair mating activity in any monogamous species.

Extrapair copulations (EPCs) have been observed in many socially monogamous species (e.g. Black-capped Chickadees [*Parus atricapillus*], Smith 1988; Northern Fulmars [*Fulmarus glacialis*], Hatch 1987), although until recently EPF detection was difficult. Genetic techniques such as DNA fingerprinting now permit accurate assessment of parentage within a social sys-

tem. Males and females of many apparently monogamous species have been shown to engage in extrapair reproductive activities (e.g. House Sparrows [*Passer domesitcus*], Burke and Bruford 1987; Indigo Buntings [*Passerina cyanea*], Westneat 1990; White-crowned Sparrows [*Zonotrichia leucophrys*], Sherman and Morton 1988; Eastern Bluebirds [*Sialia sialis*], Gowaty and Karlin 1984, Gowaty and Bridges 1991).

Clearly, equal genetic contributions to offspring tended by breeding partners (genetic monogamy) can no longer be safely assumed in socially monogamous bird species. Reported EPF rates in such species range from 0% (e.g. Northern Fulmar, Hunter et al. 1992; Black Vulture [*Coragyps atratus*], Decker et al. 1992) to greater than 30% (e.g. Indigo Bunting, Westneat 1990; Purple Martin [*Progne subis*], Morton et al. 1990; Tree Swallow [*Tachycineta bicolor*], Lifjeld and Robertson 1992). Following the recent discoveries of extrapair parentage among the offspring of socially monogamous birds, it remains of interest to identify those species in which apparent reproductive success accurately reflects realized reproductive success and to clarify the factors promoting genetic monogamy.

Species in the order Procellariiformes fulfill the conventional, hypothesized criteria for social monogamy (Wittenberger and Tilson 1980, Silver et al. 1985, Westneat et al. 1990, Mock and Fujioka 1990); they are long-lived birds characterized by long-term pair bonds, single-egg clutches, and extended periods of biparen-

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tal care during which they forage over great distances. Researchers, therefore, have routinely assumed that breeding adult procellariiforms are the genetic parents of the young they raise. We used DNA fingerprinting to assess the occurrence of EPFs in a breeding colony of Leach's Storm-Petrel (*Oceanodroma leucorhoa*).

METHODS

Study species and site.—Leach's Storm-Petrels of both sexes usually delay breeding until four or five years of age, then breed yearly for up to 30 years (C. E. Huntington unpubl. data). The female lays a single egg each year and the male and female share incubation duties during a 40- to 44-day incubation period (Gross 1935, Wilbur 1969). Adults alternate incubation bouts, during which the adult at the nest fasts for up to seven days ($\bar{x} = 3.1$ days; R.A.M. and C.E.H. unpubl. data), losing up to 7.5% of its initial body mass daily while its partner forages at sea (Ricklefs et al. 1986). Incubation is coordinated by the pair such that the egg is rarely left unattended.

The nestling is brooded for about 5 days, after which it remains alone in the burrow for 55 to 65 days. The nestling is fed during brief nocturnal visits by its parents returning from feeding areas many kilometers out to sea. Leach's Storm-Petrels are surface feeders, preying on euphausids and other zooplankton, which are concentrated in areas of upwelling and along local current clines (Haney 1985, Brown 1988, Pittman and Ballance 1990). Such oceanic feeding zones are unpredictable in space and time (Brown 1980, 1988, Duffy 1989). Thus, adult storm-petrels return to the nest sporadically, though typically a parent returns every second or third night until the chick fledges (Ricklefs et al. 1985). Parental care in Leach's Storm-Petrel lasts 100 to 110 days from egg laying to fledging.

We sampled families from the breeding colony of about 2,000 pairs of Leach's Storm-Petrels at the Bowdoin College Biological Station on Kent Island, New Brunswick, Canada (66°45'W, 44°35'N). We captured each adult storm-petrel in its burrow in late June or early July (during incubation), or in late August or early September (during the provisioning period). Presence in the burrow during either of these periods qualified an individual as a putative parent. We collected blood from chicks during the four weeks prior to fledging. We sampled 15 full families (female, male, and offspring) and 6 partial families (male and offspring) during the 1991 breeding season, and 29 full families during the 1992 season.

DNA methods.—Two 50-μl blood samples were taken from each bird by puncture of the brachial vein. During the 1991 field season, each sample was immediately suspended in 1 ml of phosphate-buffered saline (PBS; 3 mM KCl, 8 mM Na_2HPO_4, 2 mM KH_2PO_4, 0.14 M NaCl, 6 mM EDTA, 0.2% sodium azide), a nonlytic preservative. After cells had settled, the clear supernatant was removed and replaced with fresh PBS. Samples were inverted several times to resuspend cells and, subsequently, were stored at 4°C or ambient temperature for about three months. Samples collected during the 1992 season were immediately suspended in 1 ml of a lysis buffer (100 mM Tris, pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS; Longmire et al. 1988), which required no further handling.

DNA was extracted from 144 blood samples representing 44 complete families (mates plus their single chick) and 6 partial families. Extraction began with addition of proteinase K (200 μg) and SDS (to 0.8%) to each of the preserved blood samples, which were then incubated at 55°C overnight. Subsequently, four extractions were performed on the 1991 samples: one with phenol; two with 25:24:1 phenol : chloroform : isoamyl alcohol; and one with 24:1 chloroform : isoamyl alcohol. Five extractions were performed on the 1992 samples: two with phenol; two with 25:24:1 phenol : chloroform : isoamyl alcohol; and one with 24:1 chloroform : isoamyl alcohol. Following the last extraction, the aqueous phase was dialyzed extensively against TNE_2 (10 mM Tris, pH 7.4, 10 mM NaCl, 2 mM EDTA). Concentrations and purities of extracted DNA were assessed by spectrophotometry. Optical densities were determined at wavelengths of 260 nm (for nucleic acids) and 280 nm (for proteins). Estimates of DNA concentration and assessments of DNA purity were then corroborated by running 1.5 μg of undigested DNA from each individual through a 0.8% agarose gel at 80 V for about 2 h.

Gels were constructed of arbitrary assortments of families, with the three members of complete families (Fig. 1), or two members of partial families situated in adjacent lanes. DNA (5 μg) from each individual was digested with 5× excess restriction endonuclease (*Hae*III) at 37°C for about 3 h. Resulting fragments were separated through a 0.8% agarose gel (22 cm) at 20 V for 64 to 65 h (until all fragments smaller than 1,600 base pairs had been run off the gel). Fragments were then transferred to nylon by Southern blot in 10× SSC buffer and were fixed to the membrane by UV crosslinking. Jeffreys' multilocus minisatellite probe 33.15 (Jeffreys et al. 1985b, c) was radiolabelled by primer extension with [32P]dCTP. Hybridizations were run overnight at 62°C in 1.5× SSC, 0.1% SDS, 5× Denhardt's solution, and 6% w/v dextran sulfate. Hybridized filters were put through four washes of at least 30 min each at 62°C in 1.5× SSC, 0.1% SDS. Filters were then exposed to x-ray film at −20°C for at least 50 and up to 212 h (usually with an intensifying screen). A second hybridization, using Jeffreys' multilocus minisatellite probe 33.6 (Jeffreys et al. 1985b, c), was run under the same conditions and a second set of autoradiographs produced (Fig. 1).

Band-matching analysis.—We recorded the number of bands in a chick's lane that were not attributable
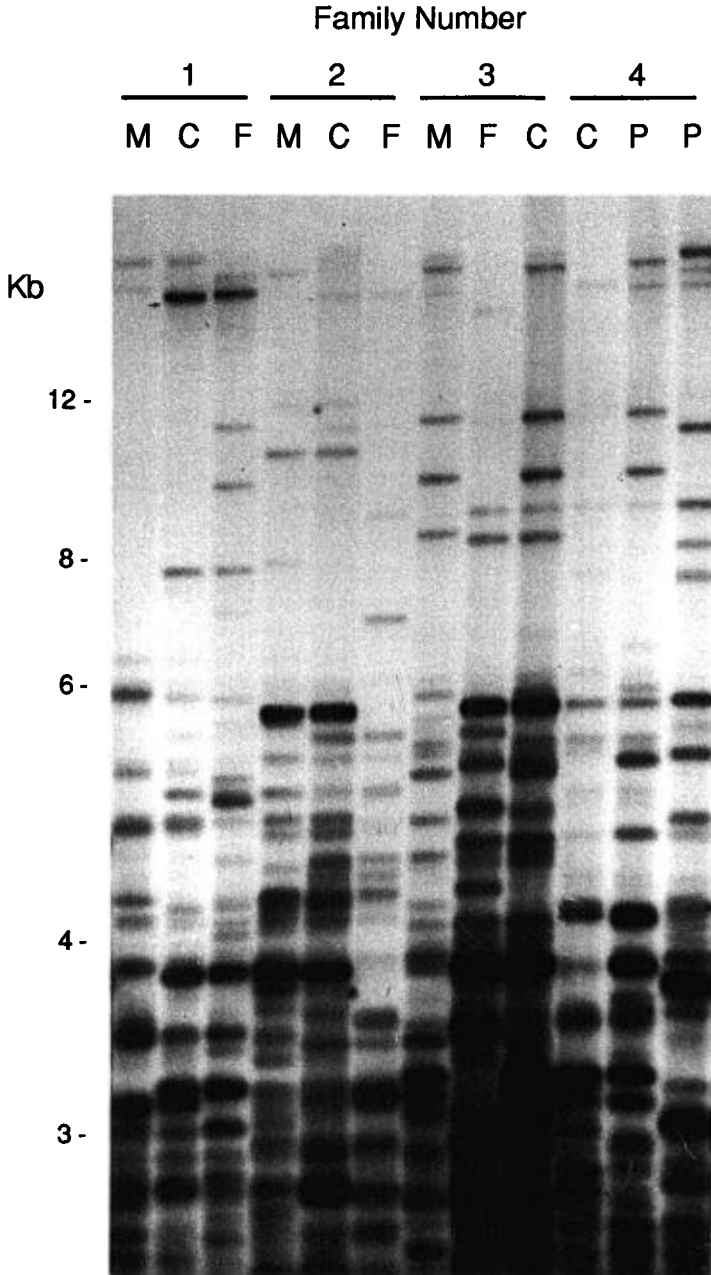
Family Number

Fig. 1. Multilocus minisatellite DNA fingerprints of 12 Leach's Storm-Petrels from four complete families (both parents and single chick) using Jeffreys' probe 33.15 and enzyme *Hae* III. Letters indicate: (M) putative male parent, (C) chick; (F) putative female parent; (P) putative parent of unknown sex.

to either of the two adults under consideration. Since all bands (or nearly all; see below) in a chick's fingerprint should be accounted for by the combined fingerprints of its parents, we compared the banding pattern in each chick's fingerprint with that of two sorts of dyads of adults. The first of these band-matching comparisons involved recording numbers of bands that were unattributable to a chick's putative parents. The distribution of such unattributable bands across the sample (Fig. 2) allows calculation of the rate of mutation (i.e. rate of appearance of bands unattributable to parental dyads; Jeffreys et al. 1988, Raben-

old et al. 1990, Westneat 1990). We applied the Poisson distribution function to the frequency distribution of the number of bands that could not be attributed to either of the putative parents (Wilkinson 1989). Thus, we evaluated the probabilities associated with various numbers of unattributable bands (Weatneat 1990) to arrive at a criterion number of unattributable bands for excluding a putative parent.

The second band-matching comparison involved recording the number of bands in a chick's fingerprint that could not be accounted for by the combined fingerprints of one putative parent and one outside adult (i.e. a putative nonparent from outside family triad). Where the sexes of the members of mated pairs were known, we selected an "outside adult" that was of the opposite sex from the putative parent. To insure independence of the data, we randomly chose one putative parent from each family for these comparisons. To minimize error in scoring due to the distance between the lanes under comparison (Piper and Parker Rabenold 1992), we always chose an outside adult whose lane was within five lanes of the focal offspring's lane, with the restriction that no lane was used more than once as an outside adult. The distribution of bands that were unattributable to either of the two adults (Fig. 2) was then fitted to a normal-distribution function, which permitted the evaluation of the probability that an outside adult could be misidentified as a parent.

To evaluate the likelihood that two or more novel bands will arise in an offspring, we first assessed the fit of the distribution of bands unattributable to putative parent dyads to a Poisson distribution (two-tailed Kolmogorov-Smirnov two-sample test, $P > 0.30$). Assuming mutations occurred randomly across individual offspring and loci, the Poisson probability was 0.013 that the combined fingerprints of the two genetic parents would fail to account for two or more bands in a chick's fingerprint, where the mean occurrence of novel bands per chick, taken as the expected proportion, was 0.17 (7 novel bands/42 chicks). Similarly, to evaluate the probability that at least two bands in a chick's fingerprint would be unattributable to the combined fingerprints of one putative parent and one outside adult, we first assessed the fit of the distribution of bands unattributable to putative parent-outside adult dyads to a normal distribution (normal probability plot, $r^2 = 0.99$, $P < 0.001$). The lower 95% confidence limit of this distribution was 1.3 unattributable bands; therefore, only rarely would the combined fingerprints of one putative parent and one outside adult account for all or all but one of the bands in a chick's fingerprint.

For any case in which one unattributable band was found in the band-matching analysis (either within putative family, or within triad composed of putative parent and an outside adult), we analyzed band matching in the corresponding autoradiograph produced by hybridization with the second probe (Jef-
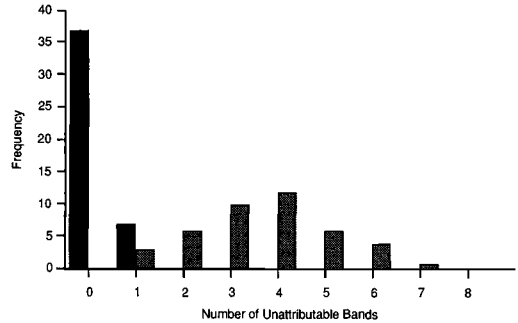

Fig. 2. Frequency distribution of number of bands in fingerprint of each of 42 Leach's Storm-Petrel chicks unattributable to combined DNA fingerprints of putative parents (solid bars), and combined DNA fingerprints of one putative parent and an outside adult (shaded bars).

freys' 33.6). We considered an outcome of one or no unattributable bands in a chick's fingerprint, summing across probes, to be an adequate criterion for the assignment of parentage.

Band-sharing analysis.—We calculated the proportion of bands shared (X_s) by each pair of individuals within each family as

$$X_s = 2S/(2S + A + B), \qquad (1)$$

where S is the number of bands of indistinguishable mobility and similar intensity in the two lanes under comparison, A is the number of bands unique to one member of the dyad, and B is the number of bands unique to the other member of the dyad (Wetton et al. 1987). The proportions of bands shared by dyads of unrelated individuals, termed "background" band sharing, can be used as a basis for comparing the similarity of banding patterns of individuals with various degrees of relatedness (Georges et al. 1988, Lynch 1990, Parker Rabenold et al. 1991, Piper and Parker Rabenold 1992). We took the distribution of the proportion of bands shared by mates to be representative of the background band sharing in the population sampled (see Discussion). While all putative parent-offspring band-sharing proportions were calculated, one randomly chosen dyad from each family was used to calculate the distribution to insure independence of the data. To corroborate the assignment of parentage based on the band-matching analysis, we then compared the distribution of between-mate band-sharing values with the distribution of putative parent-offspring band-sharing values. We performed a paired t-test to determine whether the between-mate band-sharing values and the putative parent-offspring band-sharing values (averaged over both parent-offspring dyads) represent distinct populations.

Probability of assignment errors.—Using the results from both the band-matching and band-sharing anal-

TABLE 1. Calculations of probabilities of errors in assignments of parentage based on DNA band-sharing in families of Leach's Storm-Petrels using *Hae*III and Jeffrey's multilocus probe 33.15.

	Parameter and definition	Estimate
f	Mean number bands scored per lane.	21.4
$\bar{x}$	Mean proportion of bands shared between mates.	0.58
q	Allele frequency, where $x = 2q - q^2$.	0.35
m	Expected number of maternally derived bands, where $m = f(1 + q - q^2)/(2 - q)$.	16.0
e	Expected number of paternally derived bands $= f - m$.	5.4
s	Expected proportion of bands shared by siblings, where $s = (4 + 5q - 6q^2 + q^3)/4(2 - q)$ (Jeffreys et al. 1985a).	0.77
P_U	Probability of misassigning unrelated bird as either parent, where $P_U = x^e$.	0.052
P_R	Probability of misassigning first-order relative of parent as parent, where $P_R = s^e$.	0.24

yses, we computed probabilities of assigning the wrong individuals as parents. The mean band-sharing score for dyads of unrelated individuals ($\bar{x}$ in Table 1) was used to derive, the mean allele frequency across the family of loci screened by the probe, which allows calculation of the probability of misidentifying individuals as parents (Table 1; Jeffreys et al. 1985a, Georges et al. 1988). We calculated the probability that the fingerprint of an unrelated male could account for all of the exclusively paternal bands (P_U in Table 1). The calculated probability (0.052) of misidentifying an unrelated male as the father is likewise the probability of misidentifying an unrelated female as the mother. We also calculated the probability of misassigning as a parent some close relative of the actual parent, such as a brother of the actual father. Thus, we calculated the probability that the fingerprint of an uncle could account for all of the exclusively paternal bands in the fingerprint of his niece or nephew (0.24). This probability should be multiplied by the incalculable probability that the uncle would be caught in his brother's burrow (see Discussion).

Finally, we evaluated the probability of finding no evidence of extrapair parentage in 42 complete families, as well as the probability of finding no evidence of extrapair paternity in those 42 families plus 6 partial families. Specifically, for a range of possible incidences of extrapair parentage in the population, we calculated the probability of excluding none of the nest attendents as genetic parent (E) as

$$E = 1 - Q^N, \qquad (2)$$

where Q is the proportion of chicks whose putative parents are the actual parents and N is the number of families.

Inclusion of the 6 offspring-father partial families with the 42 complete families in our analyses of monogamy in Leach' Storm-Petrel requires the assumption of no brood parasitism, a reasonable assumption given that storm-petrels lay a single egg. Any egg laid in a burrow prior to incubation presumably would be rejected by the resident female. During incubation, vulnerability to brood parasitism would be restricted to periods of egg neglect, requiring either removal of the original egg, or placing the new egg next to the original. Consequently, we would expect to find burrows containing two or more eggs simultaneously, a situation documented only six times in 35 years (>11,000 burrow-years; C. E. Huntington pers. comm.) of study on Kent Island. Brood parasitism thus has no appreciable effect on the mating system, and the inclusion of the six father-offspring dyads in our analyses seems justified.

RESULTS

Band matching.—The distributions of the numbers of unattributable bands shown in Figure 2 include those for dyads of putative parents and for dyads composed of a putative parent paired with an outside adult. For all 42 complete families, the number of bands in the chick's profile that could not be accounted for by the combined fingerprints of putative parent-outside adult dyads (median = 4) was greater than the number of bands that could not be accounted for by the combined fingerprints of the chick's putative parents (median = 0; binomial $P < 0.001$)

Among the 42 chicks from complete families, putative parents accounted for every band in 35 chicks' lanes and all but one band in the remaining 7 chicks' lanes. To corroborate our assignment of parentage in these seven cases, we analyzed band matching in those families using the 33.6 hybridization. No unattributable bands were found in any of the seven cases.

We found three cases in which the combined fingerprints of one putative parent and one outside adult accounted for all but one of the bands in a chick's fingerprint (Fig. 2). In all three cases, more than one unattributable band was found (3, 3, and 2) when the 33.6 hybridization was analyzed. None of these three cases involved any of the seven chicks whose putative parents accounted for all but one band.

With 7 of the 42 chicks exhibiting one unattributable band, the average mutation rate was calculated to be 0.17 novel bands/chick. Since, on average, 21.4 fragments were scored for each
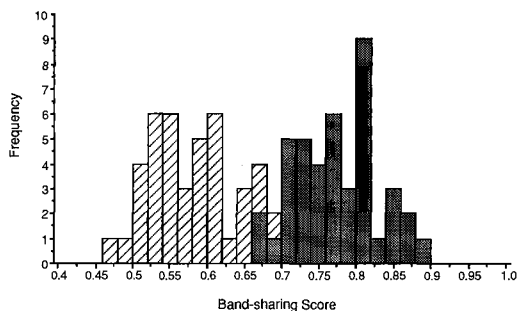
Fig. 3.   Proportion of bands in DNA fingerprint of each of 42 Leach's Storm-Petrel chicks shared with those in one (randomly chosen) putative parent's fingerprints (shaded), and proportion of bands shared between mates (diagonal).
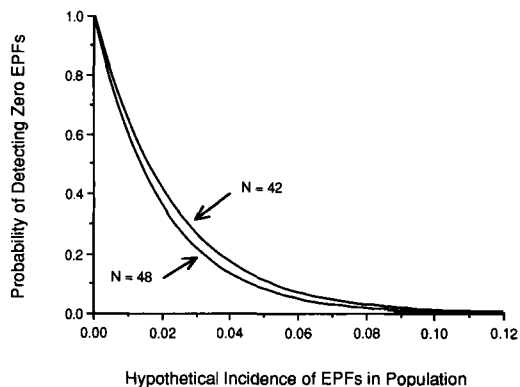

Fig. 4.   Probability of finding no evidence of extrapair parentage (i.e. zero exclusions) over range of hypothetical levels of extrapair parentage (i.e. $1 - Q$; see Methods) in Leach's Storm-Petrel population, given samples sizes of 42 (complete families) and 48 (42 complete families plus 6 partial families where DNA fingerprints of chick and its putative father were produced).

chick (f in Table 1), the per-band rate of occurrence of novel bands was 0.17/21.4 or 0.008 mutations to new-length alleles per locus per meiotic event. This rate is similar to those at minisatellite loci in other species (see Decker et al. 1992 and references therein).

Band sharing.—Figure 3 shows the distributions of band-sharing scores for dyads of first-order relatives (proportion of an offspring's bands that also occurred in each parent's fingerprint; $\bar{x} = 0.78 \pm$ SD of 0.066) and dyads of presumably unrelated individuals (the 42 mated pairs; $\bar{x} = 0.58 \pm 0.059$). Even with the 58.1% level of background band sharing ($\bar{x}$ in Table 1), first-order relatives and nonrelatives are sufficiently distinct (Fig. 3) so that the probability of misassigning a nonrelative as a putative parent is low ($P = 0.052$; Table 1). In addition, the band-sharing score for every parent-offspring dyad was greater than for the corresponding between-parent dyad, and the mean difference between these scores suggests that these dyads were drawn from distinct statistical populations (paired t-test; $t = 27.18$, $P < 0.001$, one-tailed). Five of the 84 putative parent-offspring dyads had band-sharing scores below the upper limit of the 95% confidence interval (0.678) of the distribution of between-mate band-sharing scores. Those scores involved an adult whose fingerprint together with that of its mate accounted for either all (three cases) or all but one (two cases) of the bands in the chick's fingerprint.

We used the results of the band-sharing analysis to corroborate our assignment of parentage in those cases in which one band in the chick's fingerprint could not be attributed to the combined fingerprints of that chick's putative parents (Fig. 2). In four of the seven families, both putative parents had parent-offspring band-sharing values exceeding the 99% upper confidence level (0.72) for the proportion of bands shared between presumably unrelated individuals (range 0.74–0.86). In each of the three remaining families, one putative parent-offspring dyad exceeded the 99% upper confidence limit and the remaining putative parent-offspring dyads exceeded the 80% upper confidence limit for the proportion of bands shared between presumably unrelated individuals (83, 92, and 98%; corresponding to the 2, 5, and 15% lower confidence limits for related individuals). Therefore, while the band-sharing data for these three individuals are equivocal, there is no compelling reason to exclude them as parents.

Finally, we used the results of the band-sharing analysis to evaluate whether extrapair paternity might have occurred in any of the six partial families from which blood samples were collected. The proportion of bands shared between the putative father and the chick ($\bar{x} = 0.80$, range 0.77–0.85) exceeded the upper 99% confidence limit for presumably unrelated individuals (0.72) in all six cases. Thus, we found no evidence of extrapair paternity in six partial families.

Probability of assignment errors.—Figure 4 shows the probability functions for excluding none of the putative fathers given sample sizes of 42

and 48. With a sample size of 48, if the true level of EPFs in the population were 5%, the probability that we would have excluded none of the fathers is less than 0.085. As the hypothetical level of EPFs in the population increases, the probability of finding no evidence of EPFs quickly approaches zero given our sample sizes.

DISCUSSION

Our results indicate that Leach's Storm-Petrels in our study population were strictly monogamous in that breeding partners were the genetic parents of the young they provisioned. This conclusion depends on the low probability of misassigning nonrelatives as putative parents ($P = 0.052$; Table 1). If full siblings, or parents and their adult offspring, tended to nest in close proximity, this conclusion would be suspect since the probability of misassigning a first-order relative was considerably higher ($P = 0.24$; Table 1). On Kent Island, however, natal philopatry to the island as a whole is rare ($< 1\%$ of more than 10,000 banded chicks; Huntington and Mauck in prep.). Thus, we are confident that our results are not confounded by the presence of breeding first-order relatives. If EPFs occurred at all in our study population, they apparently did so only rarely (Fig. 4).

In the population of Leach's Storm-Petrels we studied, the breeding system (genetic monogamy) matched the mating system (social monogamy). Wittenberger and Tilson (1980) predicted social monogamy when male parental care is "both non-shareable and indispensable," and when males are more successful with one mate than with two. Long commutes to ephemeral food supplies, making food difficult to obtain and deliver, are conditions under which biparental care may be obligatory (Wittenberger and Tilson 1980, Westneat et al. 1990). These conditions, therefore, are associated with monogamous mating and long-term pair bonds (Mock and Fujioka 1990).

The ecology of small procellariiforms fits this description. Biparental care may be indispensable, meaning that a single parent probably cannot successfully raise a chick. Incubation by one parent alone would result in so much neglect of the egg that hatching probably would not occur (Gross 1935, Wilbur 1969, Boersma and Wheelwright 1979). A chick that loses a parent either dies or gains mass very slowly

(Wilbur 1969, Mauck pers. obs.), the latter perhaps reducing its probability of survival to fledging (Ricklefs and Schew 1994), or to maturity (cf. Perrins et al. 1973). Parental care apparently is unshareable, meaning that one procellariiform parent cannot divide its care between two offspring successfully. No cases have been reported of a Leach's Storm-Petrel parent simultaneously raising two broods and, in brood-enlargement experiments, both the Leach's Storm-Petrel (Huntington 1963) and the closely related Fork-tailed Petrel (*O. furcata*; Boersma et al. 1980) failed to raise more than one chick.

Wittenberger and Tilson (1980) defined the conditions that would seem to favor monogamy over other mating systems. In view of the mounting evidence for EPCs and EPFs in birds, Wittenberger and Tilson's model has been expanded to incorporate the idea that the conditions that promote social monogamy also promote genetic monogamy (e.g. Westneat et al. 1990, Decker et al. 1992). In particular, Birkhead and Møller (1992) suggested that when resources become so unpredictable in space and time that two parents are required to raise offspring successfully, the pursuit of EPCs is greatly devalued. This argument assumes that pursuit of EPCs carries a prohibitive opportunity cost (i.e. allocating time to extrapair mating effort at expense of parental effort would critically reduce probability of intrapair reproductive success).

This assumption may not be valid for Leach's Storm-Petrel. Procellariiform chicks experience long and irregular periods of fasting between parental visits (Ricklefs et al. 1985, Warham 1990). Thus, it is not clear how spending relatively small amounts of time pursuing EPCs would affect chick growth and survivorship. Although we have provided evidence that EPFs are rare or absent in our study population, nothing is known of the occurrence of EPCs in Leach's Storm-Petrel. EPCs have been observed in another procellariiform, the Northern Fulmar (*Fulmarus glacialis*; Hatch 1987, Hunter et al. 1992). Hunter et al. (1992) reported that 7.2% of all observed copulations in one fulmar colony were EPCs, although they found no evidence of EPFs in 85 families. A simple extension of Wittenberger and Tilson's model (1980) to include genetic monogamy seems inadequate to explain the fulmar data or, by extension, the storm-petrel data.

A more parsimonious explanation for our failure to detect any EPFs is that last-sperm precedence and frequent copulation by mates during the female's fertile period may be sufficient to insure a high probability of fertilizing the single egg laid by the female. This mechanistic explanation is prompted by recent findings from work on other avian species. In Zebra Finches (*Taeniopygia guttata*), the last male to copulate with a female fathered 84% of that female's chicks, even when that male copulated only once (Birkhead et al. 1988). Thus, merely being the last male to copulate before fertilization may greatly increase a male's probability of paternity. In domestic fowl, Martin et al. (1974) showed that the percent of young (in a multiple-egg clutch) sired by individual males was positively correlated with the quantity of sperm delivered. In the case of the single-egg clutch, this relationship could be interpreted to suggest that a male's certainty of paternity increases with the quantity of sperm he delivers. Frequent copulations during the entire fertile period and near the onset of ovulation might greatly increase the probability of intrapair fertilization. In their study, Hunter et al. (1992) showed that male Northern Fulmars closely guarded their mates during the fertile period and immediately followed any EPCs they appeared to detect with multiple copulations of their own.

A male Leach's Storm-Petrel employing these tactics throughout the prelaying period might have a high probability of fertilizing his mate's single egg. Such tactics may be sufficiently effective to severely restrict the chance of an EPF in any given storm-petrel family and make unlikely the detection of a single EPF in 48 families. We cannot say whether genetic monogamy in Leach's Storm-Petrel reflects the rarity (or absence) of extrapair copulations, the effectiveness of male sperm competition tactics, or both. We can say, however, that for Leach's Storm-Petrels in this study population there seems to be no distinction between apparent and realized reproductive success.

Our result adds to an emerging pattern of strict (genetic) monogamy in species with small clutches (e.g. Leach's Storm-Petrel, this study; Northern Fulmar, Hunter et al. 1992; Black Vultures, Decker et al. 1992). Among socially monogamous birds, all reported occurrences of EPFs have involved species with clutch sizes greater than two. Although beyond the scope of this paper, the strategic implications of small clutch size merit careful theoretical attention in future work.

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