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Genetic monogamy in the common loon (*Gavia immer*)

Abstract We conducted behavioral observations and genetic analysis on breeding pairs of common loons in the upper Great Lakes region from 1993 through 1995 to look for behavioral evidence of extrapair copulations (EPCs) and to determine parentage of young. Pairs remained close to each other (usually within 20 m) during the pre-laying period, leaving little opportunity for EPCs to occur. Males and females both maintained physical proximity by approaching each other when they became separated. Copulations were obvious but infrequent, occurring about once every other day during the pre-laying period. Multilocus DNA fingerprinting was consistent with behavioral findings: 58 young from 47 different families were all genetic offspring of parents that raised them. Perfect genetic monogamy (genetic parentage of young by parents that rear them) in loons might arise as a consequence of the need for vigorous territorial defense to prevent territorial takeover.

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Introduction

The recent burst of molecular analysis of parentage has revealed that many socially monogamous animals, especially perching birds (Order: Passeriformes), engage in extrapair copulations (EPCs) with other, often neighboring, individuals (Westneat 1990; Gibbs et al. 1990; Stutchbury et al. 1994; Dixon et al. 1994). A number of hypotheses have been offered to explain EPCs. Females might benefit from EPCs by mating with males that are superior to their social mates in terms of genetic quality, thus acquiring superior genes for their offspring (Smith 1988; Møller 1991). Females might seek or accept EPCs as insurance against the possibility of their mate's infertility (Wetton and Parkin 1991; Wagner 1992). Finally, EPCs might benefit females through increasing genetic variability of their offspring (Westneat et al. 1990). For their part, males stand to benefit from EPCs by producing additional offspring for which another individual cares (Trivers 1972). Modern models of mating behavior have begun to incorporate costs and benefits of EPCs as a fundamental aspect of breeding strategies (Westneat et al. 1990; Birkhead and Møller 1992).

The abundant evidence for extrapair paternity in passerine birds (e.g., Westneat 1990; Gibbs et al. 1990; Stutchbury et al. 1994; but see also Gyllensten et al. 1990) has created the impression that this genetic pattern is the norm for birds generally. This perception results largely from a bias towards studies of passerines, which make tractable study animals. Before it is possible to determine the importance of EPCs to the evolution of avian mating systems, however, it will be necessary to examine parentage patterns in a broader range of avian groups. Indeed, inspection of rates of extrapair fertilization (EPF) across avian taxa (e.g., Birkhead and Møller 1992, pp. 228–229) and consideration of many

recent reports of low EPF rates among nonpasserines (e.g., Hunter et al. 1992; Decker et al. 1993; Warkentin et al. 1994; Mauck et al. 1995; Negro et al. 1996) suggests that mating systems exhibiting frequent EPFs might be largely restricted to passerines.

The common loon (Order: Gaviiformes; *Gavia immer*) is a Nearctic piscivorous diving bird. A technical refinement (Evers 1993) has suddenly made it feasible to capture and mark loons, study social behavior and investigate parentage patterns. Parentage of loon chicks is of considerable interest. On the one hand, this species exhibits extensive biparental care of young, which is often associated with genetic monogamy (Birkhead and Møller 1992). On the other hand, loons interact frequently with other adults throughout the breeding period and so have opportunities for EPCs (Rummel and Goetzinger 1975; Croskery 1988; McIntyre 1988).

An examination of potential costs and benefits of EPCs in common loons shows considerable overlap in reproductive interests between the sexes. While males would benefit from gaining EPFs with females other than their mate, cuckolded males would pay heavily because of the huge effort they expend in defending a territory, incubating eggs and rearing young. Females might also pay for EPFs if males provide care in proportion to their certainty of paternity (e.g., Burke et al. 1989; Dixon et al. 1994). However, females might benefit from EPFs as fertility insurance (since eggs are occasionally infertile; e.g., Sutcliffe 1982; authors, personal observations) or perhaps as a means of acquiring good genes for their offspring.

We regarded joint interests of male and female loons in providing extensive parental care for chicks as the single most significant factor likely to affect mating behavior. On this basis, we predicted generally that loons should be socially and genetically monogamous and specifically that males should remain close to females during the pre-laying period because of the risk of losing paternity.

Methods

Study species

While many aspects of loon behavior remain unknown because of a lack of marked adults, basic aspects of loon natural history have been worked out during the last few decades (see McIntyre 1988). Common loons winter mainly along the coast of North America and breed in freshwater from Alaska to Iceland, including most of Canada and parts of the northern United States. Males and females arrive on breeding territories within a few days of ice-off. Pair members jointly defend the territory from frequent intrusions, build a nest at water's edge, incubate two-egg clutches for 26–27 days, and feed and protect chicks for at least 11 weeks. Loons often renest following nest failures, which usually result from egg predation by raccoons or skunks (McIntyre 1977). Censuses and behavioral study of marked breeders in the upper Great Lakes region following the first major marking effort has revealed extensive breeding dispersal (movement of breeders between territories) resulting in part from frequent territorial takeover (Piper et al., in press).

Loon capture

Between 1991 and 1994, adult loons with chicks were captured at night using small motorboats and salmon landing nets (see Evers 1993) and marked with distinctive combinations of two to four leg bands (about 3 cm in diameter) made of UV-resistant colored plastic (Hermes, Inc.). After banding, blood was taken from brachial veins of adults and chicks, and 50-µl subsamples preserved at 4 °C in phosphate-buffered saline/EDTA for extraction of DNA. All birds remained alert during processing and were released together at the water's edge. Observation of newly-marked birds indicated that capture and handling had little or no effect on adult or chick survival.

Study areas

Capture, marking, blood-sampling and behavioral observations for this study were carried out in northern Wisconsin, northeastern Minnesota, and Michigan's upper peninsula. Behavioral observations were made on 24 lakes within a 13-km diameter study area in Oneida Co., Wisconsin (45°42′N, 89°37′W) and 13 additional lakes in adjacent counties (Vilas Co., Wisconsin: 11 lakes; Gogebic Co., Michigan: 2 lakes). Altogether 61 territory-years of observation were analyzed for 37 lakes. About half of the pairs studied had territories consisting of single small lakes (4–250 ha); the remainder used two or three small lakes during the breeding season (Piper et al., in press). Owing to a high rate of nesting failure among focal breeding pairs (29 successes out of 61 attempts; 48%) and uncertainty of capturing adults and chicks, there was only partial overlap (13 territory-years) between pairs for which both behavioral data and blood samples were available. Loon families on which parentage analysis was performed represented a relatively broad geographic area and 47 territory-years (40 different territories) in all: 35 from Wisconsin (Oneida Co.: 14; Vilas Co.: 15; Forest Co.: 1; Iron Co.: 5), 10 from upper Michigan (Gogebic Co.: 1; Keweenaw Co. (Isle Royale National Park): 5; Schoolcraft Co.: 2; Chippewa Co.: 1; Mackinac Co.: 1) and 2 from northeastern Minnesota (St Louis Co.: 1; Itaska Co.: 1).

Behavioral observations

From 1993–1995 we used 8 × 40 binoculars from canoe or 15–45 × spotting scopes from shore to identify loons from leg bands and to conduct behavioral observations. Most observations occurred between 0600 and 1400 hours. Identification of leg-banded loons was, in general, difficult because legs were normally submerged, but bands could be observed from up to 1 km away when legs were pulled out of water during preening or resting. In addition, bands could often be viewed underwater in good light or glimpsed when loons dove (Evers 1994). The extreme tameness of many loons facilitated identification of individuals and behavioral observations; most birds in northern Wisconsin permitted observers in canoes to view them from within 10 m without alarm. Because of the difficulty of capturing birds to mark them and the disappearance of marked birds (annual return rate of 80–85%; Evers et al. 1996), not all observed birds were marked. Altogether, for 28 of 61 pair-years of behavioral observation both members were marked (46%), for 23 only one bird was marked (38%), and for 10 neither bird was marked (16%).

Routine observations on pairs included recording of nesting behavior, courtship, copulation and interactions with territorial intruders. In addition, to test the prediction that both sexes should behave so as to prevent EPCs, we carried out scan sampling on breeding pairs from the pre-laying period through incubation from 1993 to 1995. Scan periods began at the precise moment that a loon was sighted within a known breeding territory and lasted for 1 h or until we could no longer see a loon (e.g., when both loons flew to another lake or were otherwise lost from view; mean duration of scan periods = 50.6 ± 5.0 min, *n* = 670). At 3-min intervals during each scan period, we recorded whether pair members were: (1) within 20 m of each other, (2) more than 20 m apart but still in

visual contact, or (3) out of visual contact. In addition, we recorded whether each bird was on the surface of a lake, beneath the surface (e.g., during foraging), on a nest or in flight. Although they were, in fact, often unable to see each other when submerged, we considered diving loons in visual contact if they were capable of seeing each other when they both surfaced. Scans were curtailed when one or more intruders entered the territory. At such times, we could no longer establish with certainty the whereabouts of each pair member. Since loons usually renest after nest predation or abandonment, we had scan samples for two or even three nesting attempts by some pairs. For analyses, we combined all scans for a nesting pair into a single data point.

Scan samples alone might reveal how close members of mated pairs remained to each other but could not indicate how proximity of birds was maintained. For the latter purpose, we recorded instances wherein one pair member behaved so as to maintain contact with the other. These interactions, termed "closegaps", involved clear cases of one member approaching the other after the two had been 20 m or more apart or cases wherein one member of a pair took flight after the other had done so. Closegaps were only recorded when identities of one or both pair members were known at the time of interaction or discovered shortly after. We used either leg bands or obvious sexual dimorphism (0% overlap in masses of 48 pairs captured in 1991–1994; males 26% heavier on average, range 11–57%) to distinguish between sexes in recording closegaps.

DNA fingerprinting and parentage analysis

Parentage analysis for 58 chicks from 47 territory-years was carried out using multilocus DNA fingerprinting (e.g., Fleischer 1996). Blood/buffer samples were incubated overnight at 57 °C with proteinase K and SDS, extracted twice with phenol, twice with phenol/chloroform/isoamyl alcohol and once with chloroform/isoamyl alcohol. Samples were then dialyzed for at least 24 h against 1× TRIS-EDTA. Purified DNA thus obtained was digested with *Hae*III, run in a 0.8% agarose gel for 40 h at 48 V, then vacuum-blotted (Pharmacia, Inc.) and UV-crosslinked to a nylon membrane (MagnaCharge; Micron Separations, Inc.). Membranes were hybridized at 65 °C to 32p-labelled Jeffreys' probe 33.15 and autoradiographs produced by exposure of membranes to X-ray film (Kodak XAR) with intensifying screens at −80 °C.

Parentage was analyzed using two standard procedures: (1) analysis of "novel bands" (i.e., fragments in a chick's fingerprint that were absent from its putative parents'; see Jeffreys et al. 1985), and (2) analysis of the proportion of DNA fragments shared between a chick and each of its putative parents (see Wetton et al. 1987). Scoring was done by eye and was simplified by the clarity of autoradiographs and the small size of loon families, which made it possible to compare pairs of fingerprints separated by no more than two intervening lanes. Mean ($\pm$SD) number of fragments per fingerprint was 17.0 ± 4.5 ($n = 134$).

Loon chicks that were true genetic offspring of their social parents were expected to be those with no novel fragments in their lanes, though mutations might produce one (or rarely two) novel fragment(s) in the fingerprint of a true offspring (see Jeffreys et al. 1985). True offspring were also expected to have band-sharing scores with putative parents that were well above those for pairs of unrelated individuals.

Results

Territorial intrusions

Although infrequent early in the breeding season, territorial intrusions during the pre-laying period seemed a potential source of extrapair copulations and/or intraspecific brood parasitism. Overall, intrusions occurred at a rate of 1.5 per day during the 2 weeks prior to egg-laying, 3.2 per day during the first 2 weeks of incubation and 5.3 per day during the early part of chick-rearing (data from 539 intrusions among 74 territories in 1994–1995). Moreover, 19 of 26 (73%) intrusions for which duration could be computed precisely lasted 20 min or more, so ample time seemed available for intruding males to find and copulate with territorial females. However, typical intrusions involved a series of stereotyped social interactions (e.g., circling, bill-dipping, head-bowing; see Sjolander and Agren 1972; Rummel and Goetzinger 1975) between intruder and both pair members and offered little or no opportunity for intruders to associate with pair members one on one or for intruders to approach active nests (which might have facilitated intraspecific brood parasitism). Indeed, intruders were usually stalked and attacked by pair members until they left the territory.

The fact that only 28 of 154 intruders observed in 1994 were marked, despite concentrations of marked birds in and around study lakes (45% of all territorial loons within 5 km were marked), suggested that intruders were floaters (i.e., nonbreeders lacking territories) rather than residents from nearby territories (probability of 28 or fewer intrusions out of 154 with $P = 0.45$ for each intrusion is $\ll 0.001$; binomial test).

Copulations

Copulation occurs on land following numerous subtle postures and vocalizations by a closely associated male and female (McIntyre 1988; authors, personal observations). While copulation itself takes place in plain view and lasts less than a minute, the behavioral process leading up to it requires that a pair remain undisturbed for a period of several minutes. Furthermore, no copulation seen by us or reported elsewhere has ever occurred when more than two loons were present, which suggests that the presence of more than two loons might prevent copulation. No extrapair copulation has ever been reported in loons.

Altogether, we observed 26 copulations between members of mated pairs and no extrapair copulations. Of 16 copulations observed in 10 pairs that subsequently laid eggs, 6 occurred during the last pre-laying week, 9 during the next-to-last pre-laying week, and 1 occurred 5 weeks prior to egg-laying.

We obtained a crude estimate for number of copulations per nesting attempt by dividing total observed copulations in the 2 weeks prior to all first clutches by number of minutes of observation time and then multiplying this copulation rate by total number of daylight hours in the 2 weeks prior to incubation. Thus, we estimated a mean of (5 copulations/8789 min) (12600 min pre-laying period^{-1}) = 7.2 copulations per pre-laying period, or one copulation every other day. The calculation assumes equal frequency of copulations throughout the day (see McIntyre 1988, p. 19).

Physical associations of breeding pairs

The most striking behavioral finding was close associa-
tion between members of breeding pairs throughout the
breeding season. During the pre-laying period, pairs
remained within 20 m of each other 83% of the time and
were in visual contact 99% of the time (unweighted
means of nesting attempts of 36 pairs (75 total attempts)
representing 211 h of observation; Fig. 1). In only 10 of
75 nesting attempts were males and females ever ob-
served to be out of visual contact. There was no indi-
cation that, among pairs for which data were available,
loons associated more closely during the week just prior
to the onset of incubation (7 of 15 pairs) than in earlier
weeks (8 of 15 pairs). Pairs remained significantly closer
to each other during the pre-laying period than during
incubation (22 of 22 pairs, $P < 0.01$, binomial test), at
which stage one pair member was always incubating (see
also Fig. 1). However, failed and nonbreeding pairs
spent 61% of their time within 20 m of their mates
(Fig. 1), though, again, this association was significantly
less close than that of breeding pairs during the pre-
laying period ($t = 5.1$, $df = 232$, $P < 0.001$).

The proximity of pair members to each other was
maintained by constant efforts of both sexes. Of 56
closegaps recorded in the two weeks prior to egg-laying
wherein sexes could be distinguished with certainty, fe-
males approached males in 30 cases, and males ap-
proached females in 26. In 13 pairs females approached
males more often than the reverse; in 9 pairs males ap-
proached more often ($P > 0.2$, binomial test).

Parentage

We concluded that all 58 juveniles in 47 lake-years (40
total lakes) were true genetic offspring of their social

parents (Fig. 2). This conclusion was based on two
findings: (1) occurrence of only two novel fragments
(one each in two individuals) among fingerprints of 58
offspring, and (2) high DNA fragment-sharing levels
between both putative father/offspring pairs (mean =
0.57 ± 0.09 SD, range: 0.36–0.76; $n = 58$) and putative
mother/offspring pairs (mean = 0.58 ± 0.10 SD, range:
0.32–0.76; $n = 55$). Mean band-sharing between pair
members, assumed to be unrelated, was 0.22 ± 0.12 SD,
(range: 0–0.46, $n = 37$).

For three chicks from three different lakes, no blood
had been collected from the putative mother, so only
band-sharing scores could be used for parentage analy-
sis. Scores of 0.48, 0.50 and 0.62 between chicks and
their putative fathers were taken as indications of true
genetic parentage in these cases because: (1) chicks could
only be unrelated to or true offspring of putative fathers,
and (2) these scores lie above 0.46, the upper bound of
95% confidence interval for unrelated pairs.

As a means of illustrating the robustness of our es-
timate of 0% as the frequency of extrapair parentage in
loons (including EPFs and intraspecific brood parasit-
ism), we can compute a 95% confidence interval for the
estimate as having limits of 0 and 0.063. Thus, based on
our sample, we can be 95% certain that nesting attempts
with extrapair offspring actually occur at a rate of less
than 7% in common loons.

Discussion

One potential difficulty of our study was that behavioral
observation occurred only during daylight hours. Loons
vocalize extensively at night and could possibly have
engaged in EPCs at night (McIntyre 1988). The lack of
EPFs detected by genetic analysis suggests, however,
that EPCs were rare or absent throughout the 24-h day.

Our observation of numerous unmarked loons cre-
ated two potential problems. First, any genetic mis-
matches between parents and chicks caught with them
might have resulted from undetected rapid mate-
switching rather than extrapair parentage (Birkhead and
Møller 1992). Indeed, at least six switches (three of each
sex) occurred among the 36 focal pairs, but the lack of
mismatches between adults and chicks captured with
them indicated no case in which an adult reared a chick
other than its own genetic offspring. The unmarked
birds in our sample, many of which failed in their nesting
attempts, might also have produced misleading results if
they exhibited different association patterns from
marked pairs, which more often bred successfully.
However, the sheer uniformity in behavior among the 36
focal pairs, which included pairs that were successful
and unsuccessful, marked and unmarked, left no room
for a strong bias of this kind (see Fig. 1).

A second potential problem was that pairs observed
behaviorally only partially corresponded with those
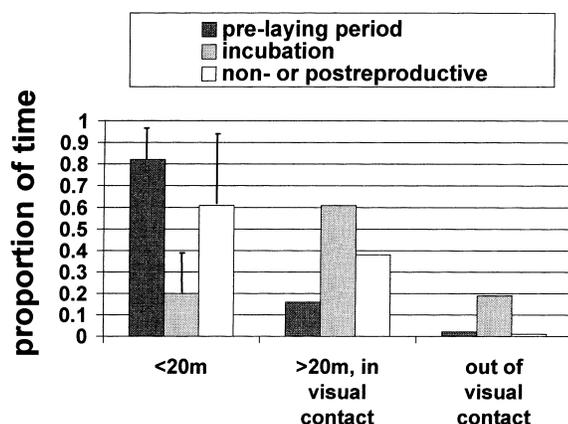whose chicks were analyzed for parentage. Again,

Fig. 1 Means of physical separation of male and female pair
members during the pre-laying, incubation and postreproductive
periods from 75 nesting attempts by 36 different nesting pairs.
Standard deviations included only for proportions of time within
20 m. Data for nonreproductive pairs were pooled with those from
the postreproductive period of breeding pairs

Fig. 2. Multilocus DNA fingerprints for loon pairs and the chicks they reared (*M* male, *F* female, *C* chick) on four lakes in northern Wisconsin and one in upper Michigan (S. Manistique). Probe: Jeffreys' 33.15; enzyme: *Hae*III. Note 19 kb fragment (indicated by *arrow*) produced by mutation in fingerprint of Nineweb Chick 2
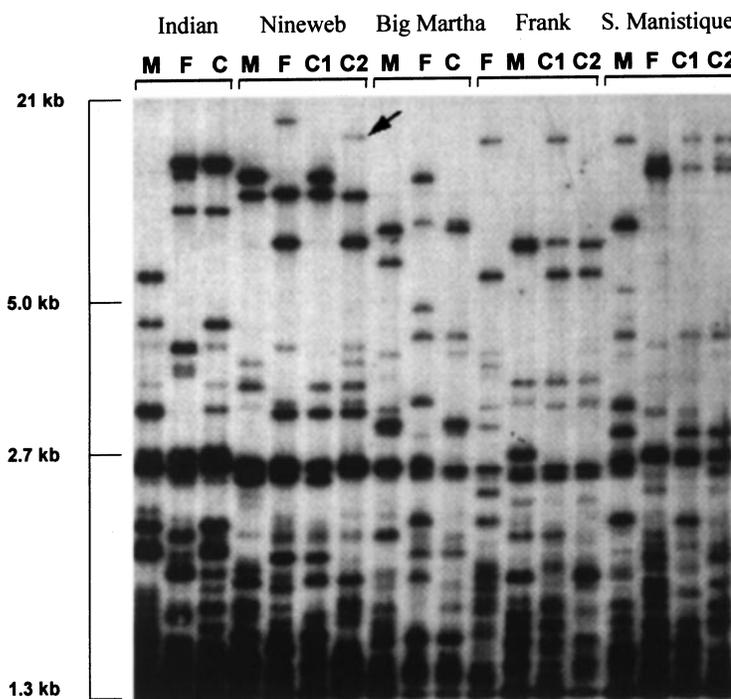
however, extreme consistency in both our molecular and behavioral findings allows us to state with confidence that loon pairs, in general, associate closely with each other during the pre-laying period and are genetically monogamous.

The occurrence of genetic monogamy in loons provides important information concerning causes of territorial intrusion. Based upon a review of the literature, Birkhead and Møller (1992) conclude that most instances of territorial intrusion probably result from efforts at extrapair copulation, rather than attempts at territorial takeover or confusion over territorial boundaries. Clearly, common loons are an exception to this general pattern. Extrapair matings and fertilizations rarely, if ever, occur in this species, and intrusions peak long after the main pre-laying period (i.e., prior to first breeding attempts). Although we are still investigating causes for territorial intrusions, they are unlikely to be efforts at extrapair copulation.

In light of the potentially high cost of EPFs to territorial males, we had expected that they might exhibit some form of paternity assurance mechanism such as frequent copulation (Birkhead and Møller 1992). This particular method was absent in loons, which copulate only about once every other day during the pre-laying period, a rate far below that of species wherein copulation is thought to serve as a paternity guard (see Birkhead & Møller 1992).

A second mechanism by which male loons could have prevented loss of paternity is by maintaining physical closeness to their mates (e.g., Alatalo et al. 1987; Dickinson and Leonard 1996). The fact that male and female loons both worked to maintain a close physical association during the pre-laying period differs from the usual tendency of males alone to maintain proximity (Hatchwell and Davies 1992; Piper and Slater 1993; Dickinson and Leonard 1996). There are at least three possible explanations for the tendency of both males and females to maintain close associations. First, males might associate closely with females to assure their paternity of young, while females associate with males for a different reason. This hypothesis would require a novel explanation for the tendency of males to remain close to females during incubation and post-reproductive periods, at which times paternity is not threatened. A second possibility is that females and males might both behave so as to reduce the frequency of extrapair copulations, thus benefitting the male by ensuring his paternity, and the female, by ensuring the male's assistance in chick-rearing. Again, this idea requires a different explanation for close association of pairs during the incubation and post-reproductive periods. Third, males and females might associate with each other throughout the breeding season for a single reason other than paternity. For example, pair members might jointly locate and attack fish schools (McIntyre 1988) or reduce the threat of predation by exploiting their mate's vigilance. We lack sufficient data to determine with certainty why males and females associate closely during the breeding season, but the idea that some factor other than paternity assurance is involved appears most parsimonious at this point.

Although it is premature to conclude that male loons used no technique for paternity assurance, it is worthwhile examining loon ecology in more detail to determine why obvious paternity guards might be lacking. The potential for social interaction that might lead to

EPCs appears lower in loons than in many other species because suitable nesting territories are often widely separated. Density of nesting territories is well-known to be correlated positively with frequency of EPCs in birds (Birkhead and Møller 1992; Møller and Birkhead 1993). Moreover, loons' large size and conspicuousness in a habitat lacking visual obstructions might prevent males and females from pursuing EPCs without being observed by their mates. A third ecological factor that might have reduced the need for paternity guards in loons is the constant threat of territorial takeover by intruders. Takeover results in the pair member of the same sex as the usurper being displaced from its territory, while its former mate pairs with the usurper. In Wisconsin, 10 of 22 individuals that disappeared from their territories between 1993 and 1996 (among 155 marked birds observed for entire breeding seasons) were known to have been displaced of their territories by intruders. Takeover results in loss of any active nest or chicks as well as loss of a breeding territory for the displaced pair member.

Given the clear threat of territorial takeover in loons, one might hypothesize that loon pairs associate closely in order to defend their territories and not to ensure paternity by breeding males. Thus, the lack of extrapair paternity in loons might have developed as a by-product of joint territorial defense to prevent takeovers. If association is related to territory defense, pairs should associate closely during the period when takeovers might occur (i.e., throughout the breeding season), and not solely during the pre-laying period. The tendency of pairs to associate closely throughout the breeding season (see Fig. 1) gives preliminary support to the idea that close association is related to territory defense. Further data showing that pair members acting in concert are more successful than lone breeders at repelling intrusions will be required to test the hypothesis completely.

Common loons (Order Gaviiformes) fall into one of the many nonpasserine orders of birds that are large, lay few eggs, require extensive biparental care during development and exhibit genetic monogamy. The intercorrelation between anatomy, ecology, behavior and phylogeny has had the result that no single explanation has emerged for the low rates of EPF among nonpasserines. We have followed most others (e.g., Westneat et al. 1990; Birkhead and Møller 1992; Decker et al. 1993; Mauck et al. 1995) in presuming that extrapair matings will occur unless males or females behave so as to prevent them and have explained the apparent absence of EPCs in loons as resulting from ecological contraints peculiar to the species. An alternative viewpoint, which becomes increasingly appealing as the number of large, genetically monogamous nonpasserines grows, is that there might be a more general explanation for the paucity of EPCs in this group. For example, birds that produce large young often must invest heavily in parental care, which might favor the development of paternity guards that ensure genetic monogamy. If so,

large species with little or no paternal care should have relatively high levels of EPCs. Clearly, we must gather data on birds exhibiting a diverse array of behavioral and ecological attributes and phylogenetic affiliations to determine if a general explanation for EPC rates is possible.

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