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Territory acquisition in loons: the importance of take-over

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We examined patterns of territory acquisition and reconnaissance in common loons, *Gavia immer*, from northern Wisconsin. Among all territory acquisitions, 41.5% occurred through passive occupation of territories left vacant after the death or desertion of a previous resident, 17% constituted founding of new territories and the remaining 41.5% came about through take-over: either usurpation of defended territories or appropriation of territories before the seasonal return of previous owners. Take-overs occurred in both sexes, but individuals acted alone, never in pairs. Displaced breeders usually took refuge on undefended lakes near their former territories; about half of these loons later regained former territories through passive occupation or took possession of new territories elsewhere. As predicted by the reconnaissance hypothesis, usurpations occurred most often in territories that had produced chicks during the previous 12 months, suggesting that loons use the presence or absence of chicks as a cue for territorial usurpation. Large individuals of both sexes held onto territories longer than small individuals, an indication that body size might be correlated with fighting ability. In terms of life history, loons appear to locate good territories through reconnaissance, usurp them in a subsequent year and recover from displacements by reclaiming their original territories or new ones.

One of an animal's most fundamental requirements is a suitable area for breeding. Animals that breed on territories must not only locate suitable habitat but compete with conspecifics for access to it. Although of obvious importance to reproductive success, acquisition of breeding territories is difficult to study in the field for two main reasons: (1) the process often occurs too rapidly for it to be described or quantified; and (2) most new territorial residents are unmarked individuals with unknown histories. However, knowledge of the behavioural context of territory acquisition and identities of individuals acquiring territories is essential for studying the evolution of strategies for obtaining breeding territories (Zack & Stutchbury 1992).

In part to overcome logistical problems of observing territorial acquisition in nature, many workers have carried out experimental removals. Rapid replacement of removed territory holders has demonstrated that many nonbreeders exist in avian breeding populations (Hensley & Cope 1951; Stewart & Aldrich 1951; Power 1975) and that prior residency often confers an advantage in maintaining ownership (e.g. Krebs 1982; Jakobsson 1988; Beletsky & Orians 1989). Removals have limited use for learning about territory acquisition, however, because they simulate only territorial turnover that occurs through sudden disappearance of a territory holder (e.g. by predation).

Studies of natural replacements have broadened our view of territory acquisition, revealing several routes whereby nonbreeders (usually young birds) gain territories. We can now define five distinct mechanisms of territory acquisition. 'Founding' is the establishment of new territories, often along boundaries of existing ones (Woolfenden & Fitzpatrick 1978; Lanyon & Thompson 1986; Birkhead 1991). 'Passive occupation' refers to taking up residence in a territory left vacant after the death or desertion of a previous resident (Eckert & Weatherhead 1987; Stutchbury & Robertson 1987), or through an organized system of queuing among unrelated (Smith 1978; Matthysen 1989; McDonald & Potts 1994; Ens et al. 1995) or related nonbreeders (Rowley 1965; Woolfenden 1975; Rabenold 1985). 'Insertion' (Arcese 1989) is the process of assuming control over a portion of the territory defended by an owner (Birkhead & Clarkson 1985; Stutchbury 1991; related to 'budding', see Woolfenden & Fitzpatrick 1978). 'Usurpation' refers to the eviction of a present, healthy territory owner from its entire territory

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(Leffelaar & Robertson 1985; Arcese 1987; Eckert & Weatherhead 1987; Ens et al. 1993). Finally, we propose the term 'appropriation' to mean occupying a territory left temporarily vacant through the tardy return of its owner from migration and then successfully resisting attempts by the owner to regain the territory upon its return (also termed 'pre-emption' by Ens et al. 1996). Although appropriation is, in fact, behaviorally intermediate between passive occupation and usurpation, here we regard both appropriation and usurpation as forms of territorial take-over.

Animals lacking territories learn about their availability and quality by living within them (Smith 1978; Arcese 1987), intruding (Arcese 1987; Stutchbury 1991), or gleaning pertinent information by means of visual or vocal cues (e.g. Beletsky 1992). Although demonstration that animals collect and later use information about territories also presents several logistical hurdles, data from a wide taxonomic array of birds suggest that they often reconnoitre for breeding areas in one year and use the information to their advantage in the next (see Zack & Stutchbury 1992).

The common loon, *Gavia immer*, is a large (3.2–5.2 kg), sexually dimorphic bird that procures fish and invertebrate prey by diving. Loons winter along the southern coast of North America, migrate singly, and breed in freshwater lakes from Alaska to Iceland, south into portions of 14 states of the U.S.A. In northern Wisconsin, loons typically occupy territories on one to three small lakes (4–100 ha; see Piper et al. 1997a) or parts of large lakes (Belant et al. 1993) shortly after ice-out in mid-April. Both pair members defend territories, but only males produce the individually distinctive yodels (Walcott et al. 1999) used in territory defence (Rummel & Goetzinger 1975). The mating system is socially and genetically monogamous (Piper et al. 1997b). Females lay two eggs in mid-May, both sexes incubate for 26–28 days (McIntyre 1988) and renesting can occur up to three times following nest failure (McIntyre 1988, pp. 26–27; personal observation). The semiprecocial chicks are fed small fish by both parents until 11–12 weeks (Barr 1996).

One of the most peculiar behavioural features of loons is the occurrence of 'social gatherings', short-term aggregations of 3–15 adults late in the breeding season (McIntyre 1988; Piper et al. 1997a). The reconnaissance hypothesis (Piper et al. 1997a) maintains that social gatherings represent efforts by nonbreeders to locate future territories. If so, territories with chicks are likely sites, because chicks might provide a reliable indication of territory quality (Piper et al. 1997a).

In the present study we examined two predictions of the reconnaissance hypothesis. First, if loons use chicks as an indication of territory quality, reconnaissance should lead to usurpation of territories that produced chicks in the previous year. Second, because the hypothesis maintains that nonbreeders use information obtained in one year to guide their efforts at take-over the next, nonbreeders should tend to visit the same lakes in consecutive years. In addition to testing these predictions, we investigated the timing and consequences of territorial take-over, which is common in loons (Piper et al. 1997b).

METHODS

We carried out research from 1993 to 1999, principally within an area measuring about 40×40 km^2 (centre of study area: 45°40′N, 89°35′W) in Oneida County near the town of Rhinelander, north-central Wisconsin. In 1993, however, study sites included four small lakes in Vilas County (ca. 45°56′, 89°25′). In all, we followed 76 different breeding territories for at least 1 year (55 for 2 or more years) on small (4–250 ha) lakes.

Basic techniques have been described elsewhere (Evers 1993; Piper et al. 1997a, b). Briefly, we spotlighted adults and their chicks from motorboats to locate and capture them during July and August of 1991–1998. We fitted loons with a metal U.S. Fish and Wildlife Service band and one to three UV-resistant coloured plastic bands (2-plex, 1/16 inch (1.6 mm); New Hermes, Inc., New York) on their legs in unique combination. Capture and marking has been shown to have no detectable effect on mortality of adults or chicks (Evers 1993).

We made visits to lakes where loons had been banded within the past 2 years to determine whether marked birds had returned (mean visit duration ± SD: 1993: 43 ± 37 min; 1994: 60 ± 32 min; 1995: 55 ± 41 min; 1996: 56 ± 36 min; 1997: 60 ± 49 min; 1998: 45 ± 35 min; 1999: 71 ± 30 min). Censuses were conducted between 24 April and 15 May (always within 3 weeks of ice-out) and consisted of visual searches for loons with 10×50 binoculars from canoe, or with spotting scopes (Bausch & Lomb, 15–45 ×) from shore, followed by identification of individuals by their leg bands. Bands were submerged during most activities, but were visible above the surface during preening and resting, wing and leg stretches, head scratching, foot waggles (one foot raised out of water, extended and shaken several times) and diving. Often, even submerged bands could be seen, when light was good. In all cases, observation of bands was greatly simplified by the tendency of most birds to tolerate approach to within 10 m by observers in canoes.

Following once-a-year censuses, we visited marked pairs every 2–8 days from about 1 May to 5 August to monitor nesting attempts, observe breeding behaviour, and record interactions between pairs and territorial intruders (mean intervals in days between visits from 1993 to 1999: 2.9, 2.1, 2.0, 4.5, 4.7, 5.0, 8.3). When possible, we also rechecked leg bands to verify that all marked birds were still on territory. On 26.5% of all visits we observed both legs of both pair members; 25.7% of the time we observed three of four legs completely; 23.8% two of four legs; 13.3% one leg; and 10.7% no legs at all (N=618 total visits; 1995 data). This frequency of loon identification made it unlikely that a marked bird's disappearance would be overlooked for more than 10 days.

RESULTS

Return Rates of Marked Loons

The most fundamental data relating to territory acquisition were the annual return rates of banded loons, which revealed the numbers of loons reclaiming past

territories and moving elsewhere. In our study area, 55 of 75 different marked birds (73%) present on territories on 31 May 1994 were still there on 30 May 1995. Thus, loons demonstrated a high degree of fidelity to breeding sites, but disappeared at a rate that indicated that factors in addition to mortality (conservatively estimated at 3%; Evers et al. 1996) were involved.

Desertion of Territories

We defined desertion as voluntary departure from a territory after at least 1 year of residence (see Ens et al. 1993). Thus defined, desertion occurred infrequently in loons. In fact, we observed only three certain cases of desertion in 6 years. In one case, a male left one territory after two failed breeding attempts and moved to a new territory 10 km away. A second male deserted a lake after nest failure to reoccupy another lake from which he had been displaced 2 years before. Finally, a female deserted a lake to take over a nearby lake following at least 1 year of nest failure. In all three cases, deserters reproduced successfully in their new territories.

Because all three cases of desertion occurred at the beginning or end of the breeding season, when our visits to lakes were less frequent, we might have failed to detect many desertions. Reasoning that failed nesters were most likely to desert (see Greenwood & Harvey 1982), we examined the tendency of breeders to return to their territories between late summer after breeding failure and the next spring. The reobservation rate of failed breeders (45 of 52 birds, 87%) was statistically indistinguishable from that of successful breeders (63 of 71 birds, 89%; G test: G_1=0.14, NS), further evidence that desertion is relatively infrequent. (In this comparison, each pair member was treated as an independent datum.)

Summary of Territory Acquisitions

Throughout the study, 98 territory acquisitions were observed, including foundings, passive occupations, appropriations, usurpations and unknown acquisitions. In contrast to a recent report of a mated pair displacing a second pair from their territory (Paruk 1999), all territory acquisitions observed during the present study involved single individuals.

For purposes of analysis, we eliminated 16 cases in which the nature of the acquisition was unknown, or a single individual was involved in a second or third acquisition. Of the remaining 82 acquisitions, 14 (17.1% of the total) resulted from foundings of seven new territories, 34 (41.5%) occurred through passive occupation, and 34 (41.5%) represented territorial take-over.

Founding of New Territories

Three of seven territories founded during the study period produced chicks. Two of these three territories were known to have produced chicks in the past 15 years but had subsequently been abandoned by breeders, while the other successful territory had an unknown history. Thus, founding is made possible by a small number of vacant territories within the population that appear comparable in quality (5 years of chick production out of 11 territory-years of breeding attempts, 45%) to continuously occupied territories (42 of 83 territory-years successful, 51%).

Passive Occupation

Passive occupation is one of the two most common means of territory acquisition in common loons. Thirty-two of 34 cases occurred as a result of the failure of residents to return to their territories of the previous season, while in the two remaining cases, loons disappeared in mid-season. These findings suggest that a substantial amount of mortality occurs during migration or in winter.

Territorial Take-over: Usurpation and Appropriation

We observed eight cases of territorial usurpation in progress and can describe the following behavioural sequence. First, an intruder lands in the territory of a breeding pair. The intruder and two pair members quickly converge, swim in tight circles on the surface and engage in many brief (5–20 s) dives (see McIntyre 1988; sketches in Sjölander & Ägren 1972). Aggression often occurs between the intruder and resident of the same sex (observed in six of eight usurpations seen in progress), which can include: (1) lunging of one bird at another on the surface; (2) grasping of one bird's bill by the other and simultaneous beating of the opponent with wings; and (3) grasping and dunking of an opponent's head. Following the defeat of a resident by an intruder, the latter pairs with the loser's mate. From time to time the new pair, especially the victorious intruder, may stalk the defeated resident until the latter leaves the territory. On occasion (two of eight usurpations seen in progress), defeated residents become unable to defend themselves, at which point they rest on shore (a behaviour never seen otherwise) and suffer further sporadic attacks. All eight observed usurpations lasted more than 1 h; one lasted more than 96 h (C. Walcott, personal communication; D. Evers, personal communication).

Two appropriations were observed in progress. In each case, an unmarked bird paired with the mate of an individual before its return from the wintering ground. Upon the tardy return of the individual, the appropriator treated the former owner as an intruder, stalking it until it left the territory. Following displacement, loons that had had their territories appropriated behaved similarly to those that lost territories through usurpation.

We used the characteristic pattern of events seen in 11 take-overs (eight usurpations, two appropriations and one take-over that could not be assigned with certainty to either class) to infer the occurrence of take-over in an additional 23 cases, in which marked breeders were replaced by new, usually unmarked, birds. The evidence we used in these assessments was: (1) appearance of a displaced resident in an undefended lake near its former territory (15 of 23 cases); (2) intrusions by the displaced

resident into its former territory or territories nearby (18 cases); (3) reoccupation of its former territory (five cases); and (4) scars or defeathered regions on the head of the displaced resident, intruder or both (two cases). In 14 of 23 instances (61%), two or more lines of evidence pointed to take-over.

Twenty-one take-overs (eight observed, 13 inferred) occurred well after ice-out and thus were clear usurpations. Two more take-overs (both observed) were clear appropriations. Incomplete data impeded our ability to distinguish usurpations and appropriations in the remaining 11 early take-overs (one observed, 10 inferred). These 11 cases were classified as 'likely appropriations'. The ice-out in 1998, which occurred 17 days before the mean ice-out during all other years from 1993 to 1999, left numerous breeding vacancies open for many days and was probably the reason why both certain appropriations and six of 11 likely appropriations occurred in 1998. In the two certain appropriations, for example, unmarked females enjoyed residency on breeding lakes for at least 12 and 22 days before resident females from the previous year returned.

Tests of the Reconnaissance Hypothesis

A critical prediction of the reconnaissance hypothesis is that usurpation should occur more often in territories that have recently produced chicks. Consistent with the prediction, usurpation showed an association with recent reproductive success. Twenty-one of 24 certain usurpations (87.5%) occurred in territories that had produced chicks in the past 12 months (G test: $G_1=5.02$, $P<0.025$; expected value of 67.8% based on total number of marked bird-years in which usurpations might have been detected). (Appropriation was excluded from this analysis because its initial stage resembles passive occupation.)

The association of usurpations with recent reproductive success might not have indicated that loons were using information about reproduction in the previous 12 months but instead that loons simply usurped good territories (determined by some other means). This possibility assumes that some territories are consistently better than others, which appears to be the case. Territories that produced chicks in a randomly chosen year ($N=37$) produced chicks with a mean annual probability of 0.645 in all subsequent years; in contrast, territories that had failed to produce chicks in a randomly chosen year ($N=19$) had a mean annual probability of chick production of 0.466 (one-tailed t test: $t_{54}=1.76$, $P<0.05$). To test the possibility that usurpations occurred in good territories rather than those with recent chick production, we classified each territory as being either good or poor, depending on whether its annual probability of chick production fell above or below the population mean (0.47; based on $N=62$ lakes and 277 lake-years). We then computed the expected proportion of usurpations in good and poor territories based on the proportion of marked bird-years in each class during which usurpations could have been detected. Of 22 independent usurpations, 13 (expected=13.66) occurred in good territories, while nine (expected=8.34) occurred in poor territories (G test: $G_1=0.1$, NS). Thus, usurpations were probably related to the production of chicks in the previous year and not to territory quality per se.

Despite evidence that chick production in a single year gives an indication of long-term territory quality, nonbreeders usurping territories that had produced chicks in the previous 12 months apparently increased their likelihood of producing chicks in the future by a small and statistically nonsignificant amount, when compared with nonbreeders choosing territories at random. Overall, 27 of 44 territories that produced chicks in one year (61%) did so the following year, while 42 of 83 randomly chosen territories (51%) did so (G test: $G_1=1.36$, NS).

The reconnaissance hypothesis posits that intruders target for take-over attempts those territories where they observed chicks during the previous breeding season. Because loons moult into alternate plumage and migrate to the breeding ground for the first time in their third year or later, 4-year-olds are the youngest class of nonbreeders that might have observed successful reproduction in a previous year, while 5-year-olds might have information from 2 years, and so forth. Thus, the reconnaissance hypothesis predicts that birds taking over territories are at least 4 years old and must have intruded into, flown over, or learned acoustically about the presence of chicks in a previous year.

Most of our data on potential reconnaissance come from adults banded as juveniles ($N=6$) 3 or more years before being observed in the study area. Five of these birds, each seen two or more times, tended to visit small clusters of lakes, and four of these returned to the same small cluster of lakes in 2 consecutive years (Fig. 1). However, only one of these birds (a 6-year-old) took over a territory, and we had no record of the bird having visited the territory the previous year. Thus, while the data provide weak support for the reconnaissance hypothesis, a thorough test will require more data.

Origins of Usurpers

Our knowledge of the identities of loons that usurped or appropriated territories is limited by the fact that most were unmarked. Among the only seven marked usurpers, one male and one female were birds from neighbouring, poorer territories; three nonbreeders (two males and a female) reclaimed territories lost within the past year; one male, which had been displaced several days before from a good territory, succeeded in usurping a good neighbouring territory; and one male usurped a good territory 6 km from where it had been reared 6 years earlier.

Characteristics of Take-over Victims

Because males (mean ± SD: 4550 ± 298 g, $N=133$) and females (3640 ± 220 g, $N=126$) vary in size, it is reasonable to expect that large loons might possess greater fighting ability or resource holding potential than small loons. If so, large loons should be better able to withstand attempts at territorial usurpation. Indeed, individuals of above-average size enjoyed longer tenure on breeding

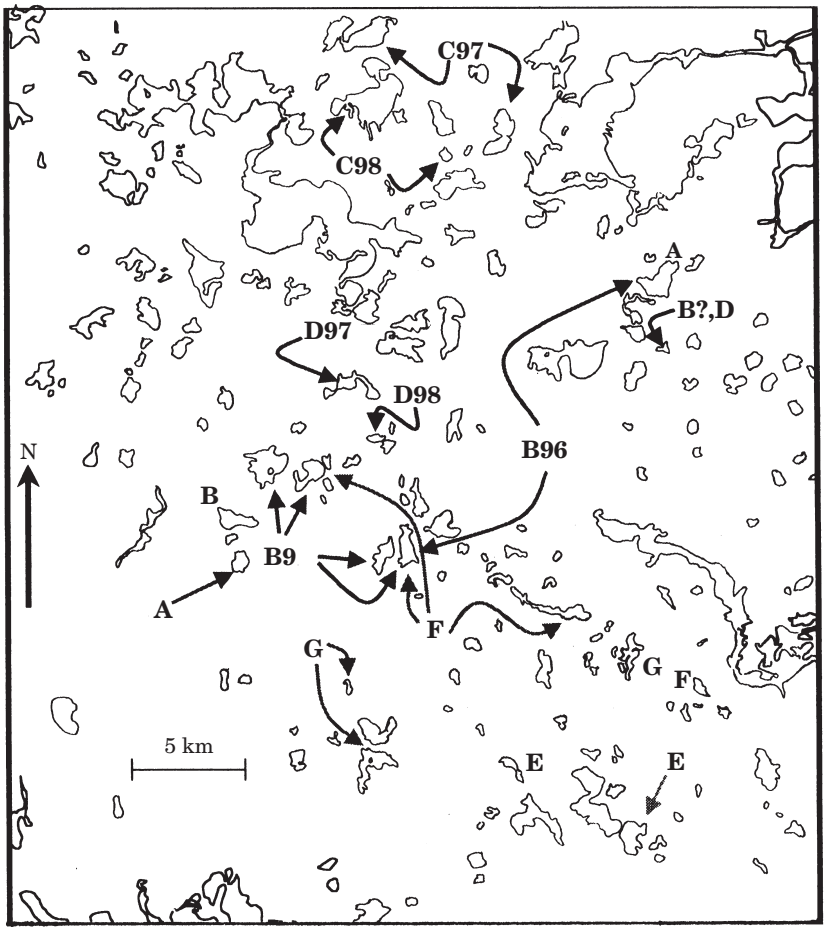

Figure 1. Sightings (large letter/year) of adults originally banded as juveniles (ABJs) in the study area. Four ABJs seen in consecutive years tended to be sighted near their natal lakes (small letters) and in the same area in each year. (Sightings of 'B' are problematic, because the same combination of colour bands was used on two different juveniles.)

territories (one-tailed Mann–Whitney U test: males: U=252, N_1=23, N_2=15, P<0.01; females: U=198.5, N_1=N_2=16, P<0.005). Moreover, loons that lost territories through usurpation (mean ± SD: males 4514 g ± 145, N=14; females: 3479 ± 150, N=6) were significantly smaller than those that experienced 3 or more years without being displaced (one-tailed Mann–Whitney U test: males: 4704 ± 390, U=144.5, N_1=15, N_2=14, P<0.05; females: 3660 ± 150, U= 65, N_1=13, N_2=6, P<0.025).

Seasonal Timing of Take-overs

Take-overs were not evenly distributed during the breeding season but instead occurred early in the year (G test: G_2=7.5, P<0.05; Fig. 2). In addition, female take-overs occurred earlier than male take-overs (Mann–Whitney U test: U=245.5, N_M=20, N_F=17, P<0.05; see Fig. 2).

Fates of Displaced Breeders

Two males seriously injured while attempting to maintain possession of their territories disappeared from the study area. Other displaced residents moved to vacant lakes nearby or began to behave as floaters, intruding into a variety of lakes in the vicinity of their former territory (Fig. 3; see also Piper et al. 1997b). Three females and two males established new territories 0.2, 0.9, 1.0, 2.0 and 5.4 km from their original territories. After five of the 31 best-documented take-overs, usurpers left territories within 8 weeks, either before (three cases) or after (two cases) attempting to reproduce there, and the displaced residents quickly reoccupied their former territories. In two additional cases, 1–2 years elapsed between displacement of and reclamation by the former owner.

Impact of Take-over on Opposite Pair Member

Although not as clearly victimized as displaced birds, the mates of displaced loons were also negatively affected by take-overs. In fact, two males and one female became victims of take-over themselves within 6 weeks of their mates' displacement. Moreover, only five of 23 breeders that lost a mate to a take-over early in the breeding season retained their own position and produced chicks with their new mate (binomial test: P<0.05; mean probability of chick production in population=0.47). Late take-overs were even more costly for mates of displaced breeders.

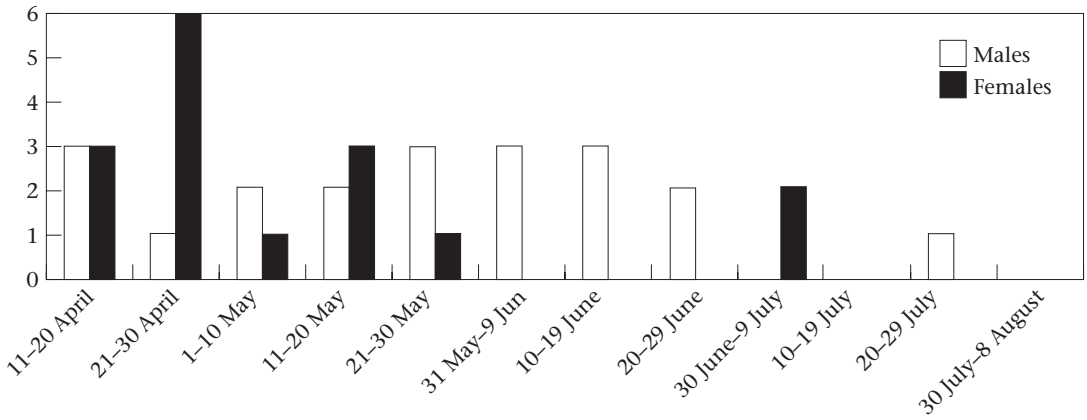

Figure 2. Seasonal occurrence of territorial take-over. Take-overs were clustered in the prebreeding period, but many males, and a few females, usurped territories later.

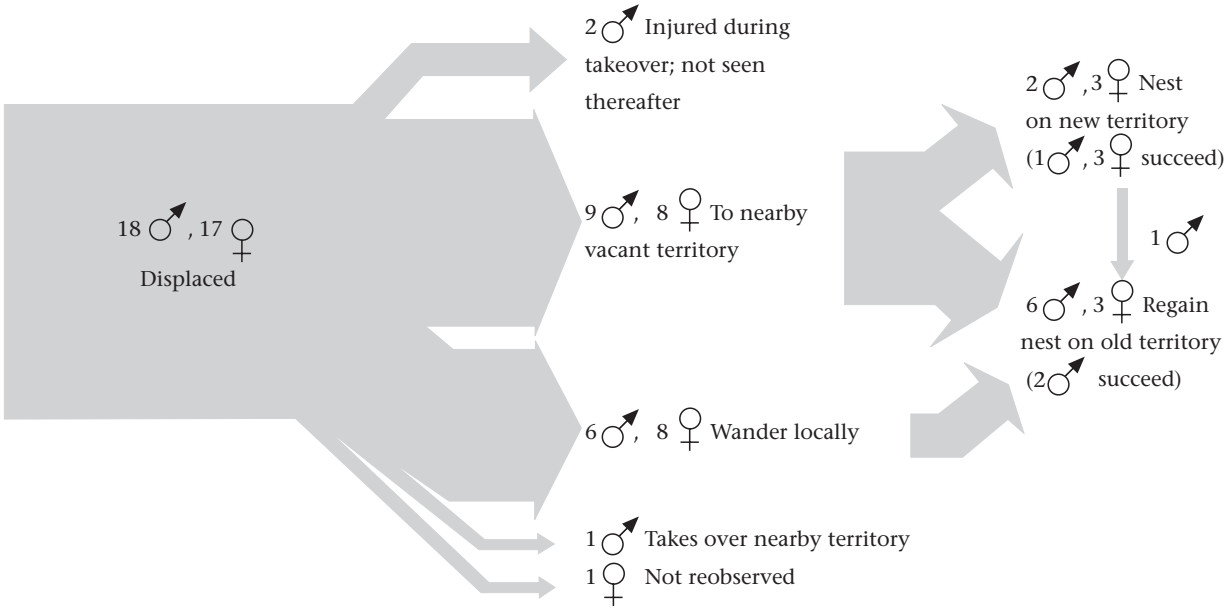

Figure 3. Fates of 29 displaced breeders whose histories were well known.

Among take-overs that occurred in territories with chicks, chicks were lost in all three cases. In 1996, a female on O'Day Lake lost her mate after a violent battle left him badly injured; she re-paired quickly with the unmarked usurper, but her 8-week-old chick disappeared within 36 h. In 1998, two 3-week-old chicks were defended for several hours by their mother on Buck Lake, but an usurping male later pecked the chicks severely and they were gone the following day. Thus, our limited evidence suggests that usurpations during chick rearing lead to chick death, sometimes through infanticide by the usurper.

DISCUSSION

Take-over of Territory or Mate?

A constant problem in studying breeding dispersal is the distinction between mate loss and territory loss. In light of the substantial differences between territories in terms of chick production, we have assumed that loons take over territories to gain access to territories and not mates. However, studies of other birds have found differences in quality among territory holders that influence reproductive success, which might drive a system of active choice for good mates (Coulson & Porter 1985; Arcese 1987). Even without differences in quality per se, mate choice might occur if loons seek compatible mates (Coulson 1966; Ens et al. 1993).

Therefore, we must examine our assumption that loons carry out take-overs to gain good territories rather than good mates. If mates are crucial to successful reproduction, then once a loon finds a mate with which it produces chicks, it should resist re-pairing. The occurrence of territorial take-over offers the mate of a displaced breeder a clear choice: to remain on its territory with a new mate, or to follow the displaced partner with

which it has reproduced successfully in the past. In 34 take-overs, we never observed a breeder to follow its displaced partner.

Although less important than a loon's attachment with its territory, we have some evidence of a 'pair bond' in loons. Occasionally pairs shift the locations of territories from one lake to another, thus changing their breeding locations but remaining with the same mates (Piper et al. 1997b; Paruk 1999). Second, in three cases, estranged mates re-paired on new lakes following independent displacements from former territories.

While take-over appears aimed at territories rather than mates, mate quality is probably important to a loon's reproductive success. Having a large mate capable of defending its breeding position might reduce the chance that a breeding attempt will be lost because of take-over, a danger heightened in loons by the long period of chick dependency. If territories are at a premium, then it is likely that nonbreeders are 'stuck' with the mate that possesses the territory at the time they acquire it. An exception to this would be cases of territory founding, in which loons could choose to pair only with large mates.

Seasonal Timing of Take-overs

Loons can breed for perhaps 20 or more years (McIntyre 1988, page 16). For this reason, a single year of breeding would appear to be worth less to them than to short-lived species, like small passerines. Thus, one might have expected that take-overs would occur not just early in the breeding season (see Nolan 1978; Birkhead & Clarkson 1985; Jakobsson 1988; Stutchbury 1991; Ens et al. 1993), when nesting was still possible, but throughout the season. Apparently the high frequency of territorial take-over and resultant brief tenure on breeding territories increases the proportional value of each breeding season for loons and causes the seasonal timing of territory acquisition in this species to resemble that of small passerines, which live for shorter periods, but seldom lose territories to usurpers.

Importance of Mates of Take-over Victims

A territorial loon whose mate's position is challenged by an intruder is not a neutral bystander to the contest. In fact, both pair members confront intruders and continue to interact with them at length during a take-over attempt, regardless of the seasonal timing of the intrusion. This suggests that both breeders resist displacement of either pair member, a behaviour pattern that seems adaptive, considering the negative effect of take-over on reproductive success in the short term.

We propose that sexual dimorphism might explain the ability of males, but not females, to achieve usurpations during chick rearing. Because they are small, females probably have little chance of outfighting a pair defending its chicks. On the other hand, a large male intruder is a good match for either pair member. As predicted, three late-season usurpations of territories with chicks were all by males, while two late-season usurpations by females occurred in territories without chicks.

Infanticide

As noted above, infanticide was observed after one take-over during the chick-rearing period and is suspected in two other cases. One might ask why usurpers kill their new mate's chicks, when this behaviour might expose them to attacks by their new mate and possibly also the parent they displaced. All but the oldest chicks, unable to feed themselves until 10–12 weeks of age (McIntyre 1988, page 43; Barr 1996), are likely to starve to death, in any event. We suggest that by taking a slight risk in killing the chicks, usurpers might curtail the chick defence of both parents, thus causing the displaced breeder to leave its territory. Hence, infanticide by usurpers might be a means of solidifying their hold on a territory. Similarly, infanticide by intruders is common even in cases wherein usurpation does not occur (Barr 1996; D. Evers, personal communication; M. Meyer, personal communication; personal observation) and might be a strategy for decreasing the aggressiveness of residents as a prelude to usurpation attempts.

The Prevalence of Appropriation in Loons

The lag of several days or weeks between the time when territories were usable and residents occupied them opened up opportunities for nonbreeders to appropriate territories. This was especially true among females, whose timing of return to breeding territories is more variable than that of males (McIntyre 1988, page 16; personal observation). Appropriation was frequent in 1998, when an early ice-out permitted many nonbreeders to occupy territories before residents had returned. Territory acquisition by appropriation occurs widely in birds, although in passerines, many would-be appropriators experience rather low rates of success, and contests are typically among males only (Lanyon & Thompson 1986; Walton & Nolan 1986; Jakobsson 1988).

The amount of time spent by would-be appropriators as residents of territories probably explains the frequency of appropriation in loons. In most birds, intruders enjoy one or a few days of residency prior to the seasonal return of the previous owner (see Lanyon & Thompson 1986; Jakobsson 1988), while loons sometimes gain uninterrupted access of up to 3 weeks. Experimental removals of territorial passerines have shown that residency of a week or more often permits an intruder to appropriate a territory (Krebs 1982; Beletsky & Orians 1989).

The advantage gained by intruding loons during residency periods, which permits them to repel the reoccupation efforts of previous residents, is not known. Perhaps, as Krebs (1982) speculates for great tits, *Parus major*, loons gain familiarity with food resources, nesting sites or neighbours within several days of occupying a territory, which could increase the value of the territory and thus their effort to maintain it.

Use of Information in Territory Acquisition

The apparent tendency of loons to assess territories in one year and usurp them the next is corroborated by a statistically significant 50% increase in intrusion rate in territories following a year of chick production (W. Piper, M. Klich, K. Tischler & T. Amrhein, unpublished data). These two lines of evidence in loons augment the growing literature on reconnaissance for breeding sites in birds (see also Zack & Stutchbury 1992). In perhaps the best-documented case, Reed & Oring (1992) showed that female spotted sandpipers, *Actitis macularia*, return to breed in areas where they have observed many potential mates in a previous year. 'Prospecting' for future nest sites is the best explanation for frequent visits by female ducks (*Bucephala* spp.) to nests of successful birds and might explain the tendency for good sites to be used in many consecutive years (Dow & Fredga 1985; Eadie & Gauthier 1985; Zicus & Hennes 1989). Apparent reconnaissance of this kind also has been reported in passerines (Stutchbury & Robertson 1987) and gulls (Porter 1988). In some other passerines (red-winged blackbirds, *Agelaius phoeniceus*; Yasukawa 1979) and grouse (Jamieson & Zwickel 1983; Wegge & Larsen 1987), nonbreeders actually establish fixed ranges late in one year that they use for breeding the next. Thus, across a broad taxonomic spectrum, birds appear to gain information about or familiarity with potential breeding areas that they benefit from in future years (see review in Zack & Stutchbury 1992).

The reconnaissance system seems flawed in that loons lose a year of reproductive effort. One might have expected loons to use permanent physical or biological features of a territory that could be readily observed in the current year as cues for usurpation attempts. Although we lack quantitative data on most such features, it is instructive to consider three obvious possibilities. Prey abundance seems to provide an unreliable indication of reproductive success, because starvation is uncommon (personal observation; but see McIntyre 1988, pp. 83–84). Similarly, the availability of nesting sites seems an unlikely cue for an intruder, because nest sites are difficult to assess and they provide only crude information about potential reproductive success. The most direct measure of reproductive success available to an intruder would appear to be the abundance of egg predators in a territory, because egg predation is the most common cause of nesting failure (personal observation; see also McIntyre 1988). However, most mammalian egg predators (principally racoons, *Procyon lotor*; see McIntyre 1988, page 24) are rarely observed during daylight hours, and the brief visits of intruders to territories afford them little chance of observing egg predators. Thus, it is possible that the presence of chicks has evolved into a cue used by nonbreeders because no more accurate means of gauging reproductive success is available.

On the other hand, the apparent use of chicks as a cue for territorial usurpation might be understood through a life history perspective. Most young nonbreeders take at least 2 years to acquire a territory (Evers et al. 1996). If young birds are prevented from gaining territories at 3 and 4 years of age because of low resource holding potential (RHP), which is a common feature in young birds (see Piper 1997), then they can afford to spend those years reconnoitring without lowering lifetime reproductive success.

If nonbreeders use an easily assessed cue like the presence or absence of chicks to guide future take-over efforts, why do they confine their intrusions to so few lakes? Intrusions to a few select territories might permit a nonbreeder to gain substantial familiarity with the breeders of the opposite sex (their future mates, if they usurp the territory), and also inspect feeding and nesting sites. Site familiarity of this kind might increase the value of the territory to the intruder and thus, its RHP there (see Zack & Stutchbury 1992). A 'shotgun' approach, wherein nonbreeders visit large numbers of territories without gaining substantial familiarity with any, might result in too small an increase in RHP in each lake to be useful in take-over attempts.

Territory Acquisition in the Common Loon

Our understanding of territory acquisition is yet incomplete. Although young nonbreeders return in consecutive years to small clusters of lakes and could acquire information that would permit them to attempt take-overs in territories that produced chicks in a previous year, they also appear to spend most of their time outside of the study area, which we infer from the paucity of observations of them in the study area despite frequent visits of observers to study lakes (Piper et al. 1997a). Croskery (1988) found that many nonbreeding loons in western Ontario remained in flocks on large lakes (1225–3966 ha), from which arrivals and departures were frequent. Such flocks persisted throughout the breeding season and showed substantial fluctuation in size in late summer, a time that coincides with the peak of intrusions into breeding territories in our study area (Piper et al. 1997b). One would surmise from Croskery's data and ours that many nonbreeders use large feeding lakes (which do exist in our study area; see Fig. 1) as bases, making occasional forays to small clusters of familiar lakes, which are potential future breeding sites.

Loons are unusual among birds in the degree to which individual differences in RHP (through body size) determine breeding tenure. Individual differences in size must have far-reaching effects. Large birds might be expected to acquire territories through take-over, whereas small birds probably rely upon passive occupation. Furthermore, while many large males and females need only acquire a good territory once, small birds must maintain possession of territories for as long as possible and recover from inevitable displacements by locating and claiming new territories, often two or more times. Small breeders must face a constant problem of collecting information about the location and availability of high-quality territories, in case of displacement. Thus, the unusually high rate of territorial take-over in loons might help explain the extensive postreproductive wandering observed in this species (Piper et al. 1997b).

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