



## Fatal battles in common loons: a preliminary analysis

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(Received 14 March 2007; initial acceptance 30 April 2007;  
final acceptance 17 October 2007; published online 28 January 2008; MS. number: A10720R)

Theoretical models predict that lethal contests should take place only when animals have severely limited breeding opportunities. Indeed, fatal fighting appears to occur routinely in only a handful of species that fit this mould. Here we report that 16–33% of all territorial evictions in male common loons, *Gavia immer*, are fatal for the displaced owner; in contrast, females seldom fight to the death for territories despite frequent territorial evictions. Since loons are long-lived and have ample reproductive options, they differ starkly from other fatal-fighting species. Several factors might contribute to lethal combat in loons, including: (1) the high value of territories to males, (2) a steady loss of condition among male residents, which could lead individuals with poor reproductive prospects to invest heavily in a current reproductive attempt, and (3) an inability of males defending tiny lakes to escape aggressive usurpers, owing to extremely high wing loading. The difficulty of detecting fatal contests in the field and the tendency of scientists to underestimate the behavioural impact of rare events leave open the possibility that fatal contests are a more widespread behavioural pattern than currently thought.

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**Keywords:** agonistic behaviour; common loon; eviction; *Gavia immer*; lethal contests; resource value; take-over; territorial behaviour

Theory suggests that fatal battles should only occur when a contested resource is of great value and individuals have severely limited breeding alternatives (Grafen 1987; Enquist & Leimar 1990). Consistent with this narrow set of circumstances, contests that result in death of one or both combatants are rarely reported in adult animals (Huntingford & Turner 1987; Enquist & Leimar 1990). Fatal battles are known to be common, however, in fig wasps (e.g. Bean & Cook 2001) and in some ants (Anderson et al. 2003), in which nondispersive individuals battle for breeding supremacy; and some spiders fight to the death for limited territories (e.g. Moya-Laraño et al. 2002). Occasional fatal fights, in the form of gang killings, also occur in primates (Goodall 1986; Palombit 1993; Gros-Louis

et al. 2003; Valero et al. 2006) and carnivores (Mech 1994; Grinnell et al. 1995; Cant et al. 2001) during territorial contests. In numerous other species across a broad taxonomic spectrum, occasional fatal battles have been documented or inferred (marmots: D. Blumstein, personal communication; caribou: Barrette & Vandal 1990; birds: Lombardo 1986; fish: Yabuta 2000; insects: Kelly 2006).

Here we report the routine occurrence of fatal battles in male common loons, *Gavia immer*, whose ecological profile makes them an unlikely candidate for this behaviour for three reasons. First, loons are long-lived, many individuals surviving 20 or more years (McIntyre & Barr 1997; W. H. Piper & C. Walcott, unpublished data). Hence, most adults stand to lose many years of breeding if they die in a territorial contest. Second, deaths and abandonments ensure a constant supply of breeding vacancies (Piper et al. 2000). Third, unpaired adults of both sexes abound (Piper et al. 2006).

Our goal in the present paper is to investigate aggressive behaviour during territorial interactions of loons, measure the frequency of fatal contests, and offer preliminary hypotheses that might explain the behaviour. A powerful tool in this investigation is a comparison with females, which, like males, invest heavily in breeding and face

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frequent territorial eviction (Piper et al. 2000), yet engage in few dangerous battles.

## METHODS

### Study Animal

Loons are large diving birds that breed on lakes mostly in northern North America and winter chiefly in coastal oceans of the continent. The species shows strong sexual dimorphism in mass ( $\bar{X} \pm \text{SD}$ ; males:  $4508 \pm 299$  g,  $N = 219$ ; females:  $3619 \pm 221$  g,  $N = 205$ ). Males are more conspicuous than females in territory defence; only males give the loud, complex yodel call during territorial interactions (Walcott et al. 1999). Males also control placement of nests and, through adaptive positioning of nests in response to successful hatches and nest predation, improve their reproductive fitness by 41% over the first 3 years of residency on a territory (Piper et al., *in press*). However, males and females jointly build nests, incubate two-egg clutches and rear semiprecocial young to 11 weeks of age (McIntyre & Barr 1997).

Territorial intrusions by both males and females are a constant feature of loon breeding ecology and average two to four per day during much of the breeding season (Piper et al. 2006). Many intrusions are efforts at prospecting by young birds; both intrusion and territorial take-over rates increase significantly following a year of reproductive success (Piper et al. 2000, 2006). Although most intruders are unmarked (1462 of 1961, 75%) and cannot easily be sexed owing to sexual monochromatism, data from marked adults indicate that the majority of intruders are females (W. H. Piper & C. Walcott, unpublished data).

There are three distinct paths to territory ownership in common loons. Many prebreeders acquire territories by passive replacement of residents that die within a pair (21% of all acquisition in males;  $N = 127$ ; 23% of all acquisitions in females,  $N = 115$ ); other prebreeders settle with a mate in vacant breeding space (28% and 30% in males and females, respectively). The bulk of all territory acquisitions, however, occur through territorial take-over, wherein a prebreeder displaces the same-sexed pair member and proceeds to breed with the mate of the displaced bird (51% of all male acquisitions; 47% of all female acquisitions; see also Piper et al. 2000). Displaced residents commonly settle on an unoccupied territories nearby, where they often pair and breed (Piper et al. 2000).

### Study Area and Capture Methods

We examined aggressive behaviour and investigated the aftermath of territorial contests in 98 breeding territories in central Oneida County, Wisconsin (centre of study area at  $45^{\circ}41'N$ ,  $89^{\circ}36'W$ ; see also Piper et al. 1997b) and adjacent portions of Vilas and Lincoln counties, which abut Oneida north and south. Eighteen loon territories comprised parts of large lakes ( $>100$  ha), 64 consisted of single whole lakes ( $<100$  ha), and 16 comprised two or more small lakes (generally 4–20 ha; see also Piper et al.

1997b). Virtually all study lakes were extensively developed and used by boaters, anglers and swimmers; most had cottages or summer camps encircling 50% or more of their shorelines.

From 1993 to 2006, we captured loons by nocturnal spotlighting from a small motorboat (see Evers 1992) and placed a unique combination of one aluminium U.S. Fish and Wildlife Service leg band and two to three coloured plastic leg bands on each adult or chick at least 5 weeks of age. Each individual was weighed to the nearest 0.01 kg. Diurnal behaviour of pairs appeared unaffected by capture; even pairs observed on mornings after having been captured and marked the previous night (i.e.  $<12$  h before) showed no discernable change in behaviour towards observers.

### Observations of Behaviour

Following one or two trips to each territory after iceout in April to confirm return of previous pair members or identify new territory owners, we made visits of 60 min or more to each breeding territory at least once weekly from 1 May through 5 August to observe loon behaviour from canoes with binoculars. We identified pair members and territorial intruders from leg bands, found any nest or chick(s), and recorded all social and vocal behaviours of the pair and intruders that occurred above the water's surface. Since adult pair members remain physically close together at all times (Piper et al. 1997a), observers could record all behaviours of pair members without use of focal sampling. We excluded from the analysis data collected on rare occasions when one pair member had left the territory temporarily (Piper et al. 1997b).

We recorded two kinds of behavioural responses related to aggression: low-level aggression and overt fighting. Low-level aggressive responses (without physical contact) involved (1) fleeing across the lake's surface by a single bird, (2) chases across the surface of a lake and (3) stalking of one bird by another, which we inferred when one loon fled from a point at which a second loon surfaced immediately afterwards. Overt fighting (with physical contact) involved (1) lunging of one bird at another bill-first on the water surface, (2) simultaneous grasping of the opponents' head with the bill by each contestant and reciprocal beating of each other with wings in an upright stance on the water's surface and (3) dunking of an opponent's head under water, which often lasted for 30 s or more. Since head grasping and wing beating were usually followed by dunking, we refer to the two behaviour patterns together hereafter as 'battles', 'fights' or 'combat'.

In the event that an established pair member disappeared from its territory, we searched all nearby lakes (which were often study lakes) for the missing bird. Thus, we could verify whether marked individuals were accounted for and appeared healthy following displacement. Our search for displaced breeders was aided by colleagues who monitor loons on breeding territories in adjacent counties, and by the public, which uses most of our study lakes intensively and commonly reports loons that appear injured to local wildlife officials.

RESULTS

Aggressive Behaviours: Frequency and Participants

In 2006, when recording of aggressive behaviour was a focal point of the study and data are most reliable, aggression was reported in 109 of 425 (26%) observation periods during which intruders were present and at a rate of one behaviour for every 4.0 h of observation. Of intrusions that resulted in aggression, 25 (23%) involved physical combat and 97 (89%) involved low-level aggression.

Males showed more of all aggressive behaviours measured, despite the apparent greater abundance of females among intruders. Behaviours that had a statistically significant disparity between the sexes were stalking (binomial test:  $X = 14, N = 15, P = 0.0005$ ; Fig. 1) and lunging ( $X = 23, N = 28, P = 0.0005$ ; Fig. 1). Battles ( $X = 13, N = 30, P = 0.29$ ) and chases ( $X = 9, N = 15, P = 0.30$ ), on the other hand, did not differ in frequency between the sexes, although both occurred more often in males.

All overt fighting that we observed occurred between opponents of the same sex and was associated with contests for status of the breeding male or female on a territory. The only hints of intersexual aggression were four instances of fleeing by females from the vicinity of aggressive males.

Injuries, Deaths and Disappearances of Territory Owners

Injuries and deaths were far more common in males than in females. Less than a week after having been observed on territory and in good health, 18 of 49 evicted

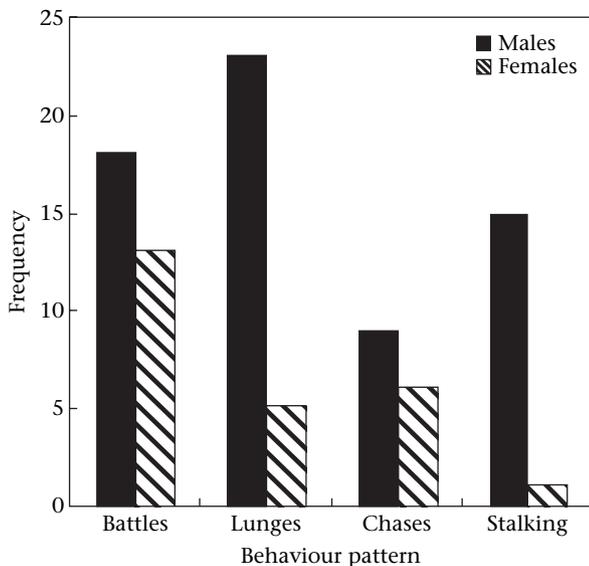


Figure 1. Frequency of aggressive behaviours by male and female loons during territorial intrusions ( $N = 853$ ) on occasions when both pair members were present.

males (37%) were missing ( $N = 8$ ), somewhat injured ( $N = 2$ ; both recovered later), severely injured ( $N = 4$ ; none reobserved afterwards), or dead ( $N = 4$ ); whereas only 3 of 28 evicted females (11%) were missing and none were injured or dead (Fisher's exact test;  $P = 0.017$ , two-sided test comparing healthy versus injured + dead + missing; Fig. 2). From these data, we can estimate the minimum frequency of fatal battles in males based only on deaths and severe injuries ( $8/49 = 16\%$ ) and a maximum frequency ( $16/49 = 33\%$ ), which assumes all disappearances were deaths.

Higher than expected disappearance rates of male territory owners between the end of our observations in one breeding season and the beginning of our observations in the next suggests fatal battles probably occurred during this interval as well. We curtailed our studies in early August each year, about half way through the chick-rearing period, and did not resume regular visits to study lakes until mid-May of the following year, at which point nesting had begun. Hence, we were unable to detect territorial conflicts during the beginning and end of each breeding season. Although we cannot exclude from this sample deaths that occurred during migration or winter, males (40 of 63 breeders not relocated; 63.5%) again disappeared with significantly greater frequency than females (27 of 62 not relocated; 43.5%; Fisher's exact test:  $P = 0.032$ , two tailed).

The sample of adult loons found dead or injured following territorial contests was small, and it consisted only of territorial males. Altogether, we found eight adult loons injured or dead following territorial contests: two were unmarked territorial males from well-documented battles with marked intruders, and the remaining six were marked territorial males. Since contests would be expected to yield an equal number of casualties among residents and intruders, these data constitute strong evidence of a bias towards injury and death among male breeders during territorial contests (two-tailed binomial test:  $X = 8, N = 8, P = 0.0078$ ).

All of our data indicate that males, not females, are the participants in lethal battles. However, we should note



Figure 2. Status and health of displaced residents following midseason eviction of residents known to be in good health at the start of season.

that fatal contests do occur, at least rarely, in females (see [Supplementary Material, Video S1](#)). Cottagers on a small lake just north of our study area acquired photographs and a carcass to document the death of a female during territorial take-over.

## DISCUSSION

### Frequency of Fatal Fighting in Loons

Our report establishes loons as one of the few animals known to engage routinely in fatal battles over resources. However, our estimate of the frequency of lethal evictions relies heavily upon males that had disappeared and were presumed dead. It is possible that some or all of these males were alive but had dispersed to lakes outside of the study area. This possibility seems remote, for three reasons. First, breeding dispersal (i.e. dispersal from one breeding territory to another; [Greenwood 1980](#)) occurs over short distances in both males ( $\bar{X} \pm \text{SD}$ :  $3.2 \pm 2.2$  km,  $N = 27$ ) and females ( $4.3 \pm 4.4$ ,  $N = 28$ ; two-sample  $t$  test:  $t_{53} = 1.17$ ,  $P = 0.25$ ), so most displaced breeders were easily relocated. Second, we routinely searched nonstudy lakes within and on the fringes of our study area for dispersers. Third, a loon researcher in Vilas County, which abuts our study area to the north, systematically identifies all adults on territory and has never recorded a former breeder from our study area on one of his lakes. Even if one adopts the highly conservative approach of viewing half of all missing males as being alive outside of the study area, roughly 24% of all male evictions in loons resulted in death or severe injury for the territory owner.

A second potential problem with our analysis relates to the cause(s) of disappearances of male loons. Although the co-occurrence of eviction and disappearance suggests fatal contests in males, high mortality of males during the breeding season for reasons other than territorial contests might have caused the high disappearance rate. However, our limited data on summer mortality in this species do not indicate a male bias. All told, we have noted six deaths of adult loons unrelated to territorial behaviour. Two females died while incubating; one was attacked by a bald eagle, *Haliaeetus leucocephalus*, a second by a mammal, probably a fisher, *Martes pennanti*. A third female is also suspected to have died on the nest. A fourth female died of lead toxicosis after ingesting a fishing sinker. Among males, one certainly died after a fishing lure ensnared its foot; a second male probably died through entanglement in fishing line.

Our finding of frequent fatal battles among loons is confirmed by necropsy data from multiple reports. These data are uneven, as determination of causes of mortality depend upon the quality of the carcass and the investigator's experience and knowledge of loon ecology. Nevertheless, [Pichner & Wolff \(2000\)](#) reported about 20% of all adult loons they examined from Minnesota had died from bill spearing during intraspecific aggression. [Franson & Cliplef \(1992\)](#) attributed 10% of all adult deaths from trauma in Minnesota ( $N = 30$ ) to the same cause. Based on a sample from New England, [Miconi et al. \(2000\)](#) found that 4 of 15 (27%) adult loon deaths from

trauma were caused by conspecifics, indicated by lacerations on the head and neck and punctures to the torso consistent with bill spearings by conspecifics. Clearly, these studies support our finding that fatal contests are an important source of mortality in loons, although incomplete data on sex make it impossible to determine the sex ratio among the victims.

### Does Sexual Selection Theory Explain Male Aggressiveness?

A curious aspect of territorial behaviour in loons is that only males commonly escalate battles to the point of death. Sexual selection theory appears not to explain this pattern, as male and female mating success are both equally dependent upon securing and maintaining a territory ([Piper et al. 2000](#)), without which breeding cannot occur. Two behaviour patterns suggest, moreover, that mate choice is of little consequence in territorial disputes. First, territorial contests are one-on-one scuffles between a breeder and an intruder; the breeder's mate is always a passive observer. Second, in all 63 well-documented evictions during the study, the mate of the displaced breeder remained on territory and paired with the usurper, rather than following its evicted mate to another territory (see also [Piper et al. 2000](#)).

### Are Fatal Fights Truly Rare in Animals?

It is tempting to accept the widespread belief that fatal fighting is rare in animals ([Huntingford & Turner 1987](#); [Enquist & Leimar 1990](#)), conclude that loons are atypical, and look for the peculiar suite of factors that caused the behaviour to evolve in this species. Before doing so, however, we must note the difficulty of detecting fatal contests. There are three chief means by which field studies can detect lethal battles: (1) observation of battles themselves; (2) finding of severely injured animals or carcasses that bear wounds from battle; (3) recording of disappearances that coincide with territorial displacement in species that show very limited breeding dispersal. While large, diurnal animals that dwell in open areas may engage in battles that can be detected easily (e.g. [Barrette & Vandal 1990](#)), other species fight at times or in habitats that preclude observation (e.g. [Kelly 2006](#)). In addition, the presence of observers may alter social behaviour (e.g. [Caine 1990](#)) in a way that reduces the likelihood of fatal battles or disrupts battles in progress. Furthermore, carcasses resulting from deadly battles often disappear quickly ([Ward et al. 2006](#)) or are missed ([Osborn et al. 2000](#)). Hence, we should not presume that fatal contests will be detected easily in species where they occur.

An additional problem we face in determining the frequency of fatal fighting in animals is an understandable tendency of field workers, and those interpreting their data, to avoid calling attention to dangerous battles documented incompletely or observed rarely ([Arcese 1987](#); [Piper et al. 2000](#); [Yabuta 2000](#); [Kelly 2006](#)). Yet, deaths from conspecific fighting, while rare from the

standpoint of a field observer, can have a substantial evolutionary impact on behaviour, especially in long-lived species.

### Evolution of Fatal Fighting in Loons

The ultimate cause of fatal fighting in loons is not obvious. Vacant territories and unmated females are constantly available, so both territory owners and residents would appear to have ample reproductive options in the event that they lose a territory (see Grafen 1987). Nor are fatal fights opportunistic like those of many mammals, which only launch dangerous attacks when they outnumber an opponent (e.g. Goodall 1986; Valero et al. 2006). Thus loons seem not to fit within fatal-fighting theory, in its current form (Enquist & Leimar 1990; Watts 2004).

Site familiarity, which improves fitness of males during their territorial tenure owing to their ability to learn and remember safe nesting sites (Piper et al., *in press*), constitutes an asymmetry in resource value that could motivate owners to fight hard to defend their territories (Maynard Smith & Parker 1976; Leimar & Enquist 1984; Enquist & Leimar 1987). A causal link between site familiarity and fatal fighting seems plausible, because females, which rarely fight to the death, do not achieve site familiarity of this kind (Piper et al., *in press*). Yet the fitness benefit of site familiarity for a resident male, a 41% increase in reproductive success from the first to third year (Piper et al., *in press*), appears small relative to the cost of dying in battle and losing many potential years of reproduction on a new territory.

Another potential motivator of risky fighting in resident males, which tend to be old, is their low residual reproductive value ('RRV': see Williams 1966; Kemp 2006). If older males experience a loss of condition with age to the point where their RRV is close to zero (i.e. they stand little chance of moving elsewhere and breeding successfully there in the event of displacement), they should invest heavily in a current reproductive attempt (Velando et al. 2006), including defence of the territory. Rigorous testing of this 'terminal investment hypothesis' is beyond the scope of this paper, but preliminary data support it. As predicted, male territory owners tend to lose mass between years ( $\bar{X} \pm \text{SD}$  change for males =  $-77 \pm 178$  g;  $N = 46$ ), while females tend to gain mass ( $+62 \pm 158$  g;  $N = 30$ ;  $t$  test:  $t_{74} = 3.46$ ,  $P = 0.0009$ ). However, we had multiple weighings for only six young male owners of known age and thus cannot yet rule out the possibility that mass loss occurs in all males, rather than old males only.

While it is plausible that adaptive site familiarity, loss of body condition or some other factor motivates territorial residents to fight for territories, intruders too must be willing to escalate contests in order for dangerous battles to occur. The fact that only owners die in fatal fights seems a crucial clue, as it suggests that usurpers have superior fighting ability. (This inference is further supported by the loss of mass among male residents as they age.) An asymmetry in fighting ability might lead intruders to escalate contests with owners (Leimar & Enquist 1984). A second factor of likely importance is the ability of

intruders to assess territory quality by means of prospecting (Piper et al. 2006), which increases the value of the resource to them. Finally, honest signalling of body size and condition (Mager et al. 2007) might contribute to contest escalation by permitting intruders to target owners that they are likely to defeat in battle.

### Failure of Losers of Battles to Escape

Even if, as we propose, intruders and owners have counterbalancing motivations that explain why they participate in battles, we must still explain why battles proceed to the point of death. For their part, victorious intruders are relentless in their pursuit and attack of weakened residents. Such behaviour seems adaptive; residents that survive sometimes succeed in evicting in a later year the intruder that had displaced them (Piper et al. 2000). The behaviour of vanquished residents is harder to understand. One would expect that, as the outcome of a battle becomes clear, a defeated resident would take refuge on a neighbouring, undefended territory (Piper et al. 2000). Indeed, fatal contests often consist of sporadic combat that lasts for many hours or days and would appear to permit ample opportunity for escape. That losers do not do so suggests two possibilities. First, males might be unable to assess their likelihood of winning contests and therefore often allow contests to escalate to the point of serious injury. Second, males might lose the capacity to become airborne after initial severe battles and thus be doomed to suffer repeated attacks from their opponents, in the event that they cannot escape the territory by swimming. The latter hypothesis seems plausible in loons, as they have among the highest wing loading of all birds (Savile 1957) and must often run for 100 m or more across the water before acquiring sufficient lift to take flight. A clear prediction from this hypothesis is a higher incidence of fatal battles on lakes small enough that they contain no extraterritorial space in which a displaced resident can hide. Future data collection on lakes of various sizes will permit a robust test of the hypothesis.

### Acknowledgments

Funding was provided by the National Science Foundation, National Geographic Society, Environmental Protection Agency, Disney Conservation Fund, Sigurd Olson Environmental Institute, North American Loon Fund, Chapman University and Cornell University. Harold Dyck and Rita Petersen of the UCI Center for Statistical Consulting provided helpful guidance concerning statistical tests. The following research assistants contributed to this study: Keren Tischler, Margaret Perala, Nathan Banfield, Marc Schwabenlander, Amy Turcotte, Erin Harrington, Eric Witham, Tim Larsen, Eric Coonradt, Julie Mao, Len Liu, Curt Jacoby, Michele Parara, Michael Nelson, Peter Keith, Curan Bonham, Kristen Potter, Ainsley Seago, David Latremouille, Michelle Gojkovich, Brad Lampe, Duncan Reid, Matthew Gibbons, Rachel Hart, Alyson Webber, Carly Michie, Mandi Reiman, Jason Reiman, Elizabeth Summers, Jesse Schwingle, Max Bockes, Ehren

Banfield, Erin Snell, Kristin Pufpaff, Jessica Ciske, Lauryn Linsell, Jessica Walden, Ben Rubin and Bethany Glaeser. We thank many landowners who provided access to their lakes.

### Supplementary Material

Supplementary material for this article may be found, in the online version, at doi:10.1016/j.anbehav.2007.10.025.

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