



Fatal battles in common loons: a preliminary analysis

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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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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 ± 299 g, $N = 219$; females: 3619 ± 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.

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