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Jeremy A. Spool
*University of Wisconsin-Madison*

Lauren V. Riters
*University of Wisconsin-Madison*

Walter H. Piper
*Chapman University*, wpiper@chapman.edu



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# Investment in Territorial Defence Relates to Recent Reproductive Success in Common Loons (*Gavia immer*)

# Investment in territorial defence relates to recent reproductive success in common loons (*Gavia immer*)

Jeremy A. Spool[1], Lauren V. Riters[1], Walter H. Piper[2]

[1]Department of Zoology, University of Wisconsin, Madison, WI, USA

[2]School of Earth and Environmental Sciences, Chapman University, Orange, CA, USA

**Corresponding author:** Jeremy A. Spool, Department of Zoology, University of Wisconsin, Madison, WI, USA. E-mail: spool@wisc.edu

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# Abstract

As the value of a limited resource such as a territory increases, animals should invest more in the defence of that resource. Because reproductive success often depends on the quality of a breeding territory, reproductive success or failure may alter the perceived value of territory and affect an animal's investment in territorial defence. We used common loons (*Gavia immer*) to test the hypothesis that animals with recent breeding success would show stronger territorial defence than those with no recent breeding success. Surprisingly, successful loons responded less, not more, to a simulated intrusion. However, birds with success in the previous season also increased their territorial response as the breeding season progressed. In conjunction with past data showing that recently successful loons experience an increase in conspecific intrusions on their territories, we interpret our data to suggest that loons with recent success offset the cost of increased intrusions by adopting a more efficient strategy for territorial defence (e.g., limiting investment in resource defence until the time of the season when it is most critical).


**Keywords:** breeding success, common loon, resource value, territory

# Introduction

Territorial defence is costly but essential for many animals to breed (Brandt, 2003; Clutton-Brock, Albon, Gibson, and Guinness, 1979; Neat, Taylor, and Huntingford, 1998; Piper, Walcott, Mager, and Spilker, 2008a). To maximise fitness, investment in territorial defence must be proportional to the value of the territory. For example, while intruders seeking to usurp a territory may injure or exhaust the defending resident, potential mates or food resources on the territory may justify costly defence (Dearborn, 1998; DiMarco and Hanlon, 1997). In general, territory owners expend less energy defending a poor quality territory than a good one (Arnott and Elwood, 2008; Enquist and Leimar, 1987), as illustrated by increased territorial behaviour in response to experimental increases in food abundance (Dearborn, 1998; Foltz et al., 2015), territory size (Lindström, 1992) and the presence of mates (DiMarco and Hanlon, 1997). However, the ultimate consequence of defending breeding territory is a successful or failed attempt to produce offspring.

Non-breeding animals tend to choose future breeding habitat by observing where conspecifics successfully raised offspring (Boulinier and Danchin, 1997; Brown, Brown, and Danchin, 2000; Doligez, Danchin, Clobert, and Gustafsson, 1999), and past studies in wrasses (*Symphodus ocellatus*; (Alonzo, 2004)) and common loons (*Gavia immer;* (Piper et al., 2006)) show that territory owners with a recent history of producing offspring attract more intruders than owners with no recent offspring production. This suggests that recent breeding success of owners may increase the perceived value of a territory to conspecifics. Additionally, territory owners use their own recent breeding success or failure as a method of habitat selection, reusing nest sites that resulted in breeding success, and avoiding nest sites that resulted in breeding failure (Haas, 1998; Hoover, 2003). This raises the possibility that an owner's recent breeding success on a territory increases the perceived value of that territory to the owner, leading the owner to increase defencive behaviour. Here we test the hypothesis that owners respond to their own recent breeding success on a territory by investing more in its defence.

Common loons show high fidelity to breeding lake territories, which they defend using territorial calls and physical confrontations with conspecific intruders (Piper, Walcott, Mager, and Spilker, 2008b; Sjolander and Agren, 1972). Nesting pairs experience approximately three conspecific intrusions a day during the breeding season (Piper et al., 2006) and sometimes pay heavy costs during territorial battles, which can be fatal for resident males (Piper et

al., 2008a). We performed simulated territorial intrusions and compared behavioural responses of male loons that had successfully produced chicks in recent breeding seasons to those that had not. We also examined how male age and the duration of the resident pair bond relate to territorial defence, as older animals may invest more in territorial defence (i.e., the Terminal Investment Hypothesis (Pianka and Parker, 1975)) and to control for the possibility that loons may be defending access to their mates (if owners are evicted, mates pair with the usurper (Piper et al., 2000a; Walcott, Mager, and Piper, 2006)).

# Methods

**Study species and area**

We conducted single trials on 50 male loons that had owned and remained on a single territory for at least two years (i.e., 2014 and 2015) prior to the year of the study (i.e., 2016). The life histories of all 50 focal males were well-documented due to a long-term study of this population (Piper et al., 2015; Piper et al., 1997b). Because about 48% of loon nests successfully hatch chicks (Piper et al. 2008b; chief cause of failure is predation by raccoons, *Procyon lotor* (McCann, Haskell, and Meyer, 2004)), many loons vary in their breeding success from year to year. When intruding on established territories, conspecifics do not solicit extra-pair copulations and rarely forage (Piper et al., 2006; Piper et al., 1997a). The primary purpose of intrusions is to assess territory owners, or to usurp the territory (Piper et al., 2015).

Territories consisted of entire small lakes (N=40; mean area ± SD: 55 ± 36 ha) or protected bays of large lakes (N=10; mean size ± SD: 358 ± 347 ha) within an 800 $km^2$ region in northern Wisconsin (centre: $45^{O}$42'N, $89^{O}$36'W; Piper, Grear, and Meyer 2012).

**Simulated Territorial Intrusions**

A single observer in a canoe recorded behavioural responses of loon pairs to a simulated territorial intrusion (STI) using a wooden loon decoy chosen to resemble the size of an average adult male loon (height: 24.13 cm; width; 24.13 cm; length: 53.34 cm in a neutral swimming position). All trials were conducted in the pre-nesting phase of the breeding season in 2016, between April 16$^{th}$ and May 3$^{rd}$, before any loon eggs were observed in the study area. First, the identity of pair members was verified using their coloured leg bands. The observer then paddled to approximately 50 m of the pair members, turned, and anchored the wooden loon decoy in the water so the focal pair could not see it (obscured by the canoe). The observer then paddled forward to reveal the decoy to the

loons and started the trial the moment a resident turned towards the decoy. At the moment the trial began, a seven second territorial yodel was broadcast twice using a Bluetooth speaker (Nuu Wake Waterproof Bluetooth Speaker, Noetic Inc.) from the canoe. These calls are emitted by males during agonistic encounters (Mager, Walcott, and Piper, 2012), and were recorded from a male in the study area who has been deceased for 13 years. At the time the yodel was broadcast, the decoy was situated in between the canoe and the resident pair; the canoe was approximately 5-10 m from the decoy. Male loons normally yodel in a crouched position (Mager and Walcott, 2014). While our wooden decoy is fixed in a neutral swimming position, all loons tested were exposed to this same simulated intrusion and all loons approached the decoy during trials. Following playback of the yodels, the observer in the canoe observed behavioural responses from a distance of 10-15 m to the decoy for the duration of the trial. Responses to the decoy were recorded for 15 minutes, or ended when both pair members moved >50 m from the decoy.

During trials, the observer recorded the time (in seconds) the loon pair spent within 10 m of the decoy (a general measure of territorial behaviour that reflects the amount of time resident loons invested attending to the simulated intruder (Jukkala and Piper, 2015)), the number of splash dives, bill dips, excited peering, circle dances, and times the focal male surfaced within 1 m of the decoy. The observer also recorded all vocalisations (including toots, which are emitted by pair members in response to intruders, and yodels by the resident male) and the number of times residents physically attacked the decoy (by lunging, pecking, or beating with wings).

**Test variable definitions**

In order to test the extent to which recent breeding success alters territorial behaviour, we first focused on comparing male loons that raised at least one chick to fledging in either of the two previous breeding seasons (Success within the last 2 years) to males that did not (No success within the last 2 years). We first focused on this definition of breeding success because we reasoned that a single failed breeding season (i.e., no chicks produced) would not necessarily have a negative impact on territory resource value to resident males, as only 48% of nests hatch chicks (Piper et al., 2008b). However, we also performed separate analyses comparing males that had raised at least one chick to fledging during the previous year only (Success last year) to males that were unsuccessful in the previous breeding season (No success last year), because it could be that the previous breeding season is most salient to male loons in assessing territory value.

We defined pair territory tenure as the number of consecutive seasons a pair was territorial together on its current lake. Age was known exactly for 19 males initially marked as chicks; age was estimated for the remaining 31 males banded as adults by assuming five years of age at banding, which is the average age at which males first settle on territories in the study area (Piper et al., 2012).

# Statistics

We first ran two general linear models using time spent within 10 m of the decoy as the dependent variable. The first model used "Success within the last 2 years", age of the male, and pair territory tenure as predictor variables. The second model used "Success last year", age of the male, and pair territory tenure as predictor variables. To ensure that time spent within 10 m of the decoy reflected the loons' territorial response to the decoy (and wasn't simply a response to novelty), we ran an additional model identical to the first model described above, except the total number of behaviours directed towards the decoy (sum of splash dives, bill dips, excited peering, circle dances, and the number of times males surfaced within 1 m of the decoy) was entered as the dependent variable. We finally ran a model using identical predictor variables to the first model described above, but using the number of toot vocalisations as the dependent variable.

During decoy trials, the experimenter noted that territorial behaviour seemed to increase as the breeding season progressed. To test this possibility, we ran parallel linear models that used either "Success within the last 2 years" or "Success last year" as a predictor variable, and date of trial (number of days before the first reported egg in the 2016 season) to predict time spent within 10 m of the decoy.

A subset of individuals (n=30) in the current study had been exposed previously to the decoy without yodel playback in the 2012-2013 breeding seasons (3-4 years prior to the present study; Jukkala and Piper, 2015)). To account for the possibility of habituation, we included as a predictor in all analyses whether either pair member was previously exposed to the decoy.

Pair territory tenure was unknown for six pairs due to the unknown identity of the female pair member. All models and post-hoc pairwise comparisons returned similar results whether these six data points were included or excluded. Therefore, we report models including pair territorial tenure (excluding six data points), and report post-hoc pairwise comparisons including all available data.

We constructed QQ plots of residuals to assess normality and fitted values by residual plots to assess homogeneity of variance. All models met the assumptions of parametric statistics.

# Results

**Recent breeding success, pair tenure, age, and past exposure to decoy**

The model predicting time within 10 m of the decoy revealed significant main effects of success within the last 2 years ($F_{1,32}$=7.671, p<0.0093), past exposure to the decoy ($F_{1,32}$=7.767, p<0.0089), and territory tenure of the pair ($F_{1,32}$=5.85, p<0.021). Post-hoc pairwise comparisons revealed that male loons spent less time within 10 m of the decoy if they had success within the last 2 years ($t_{48}$=3.19, p<0.0025; Fig. 1) and if they had been exposed previously to the decoy ($t_{48}$=2.838, p<0.0066; Fig. 1). A simple linear regression with territorial tenure of the pair as an independent variable and time within 10 m of the decoy as the dependent variable revealed that loons with longer tenure on the same lake spent less time within 10 m of the decoy ($r^2$=0.14, $t_{42}$=2.62, p<0.0122; Fig. 1).

The model using success last year as a predictor variable revealed similar, though weaker main effects (success last year ($F_{1,32}$=3.224, p<0.082), past exposure to the decoy ($F_{1,32}$=7.007, p<0.0125), and territory tenure of the pair ($F_{1,32}$=5.453, p<0.026). Additionally, there was a "Success last year" by male age interaction ($F_{1,32}$=7.223, p<0.012), but male age did not correlate with the time loons spent within 10 m of the decoy in either males with success last year or males without success last year ($r^2$<0.065, p>0.2).

The model using the total number of behaviours pairs directed towards the decoy produced nearly identical results, with significant main effects of success within the last 2 years ($F_{1,32}$=6.71, p<0.0144), past exposure to the decoy ($F_{1,32}$=8.47, p<0.0144), and territory tenure of the pair ($F_{1,32}$=5.23, p<0.0290). Additionally, the total number of behaviours pairs directed towards the decoy was highly correlated with time spent within 10 m of the decoy ($R^2$=0.581, p<0.001). Thus, to avoid redundancy, here we focus on results for the time loons spent within 10 m of the decoy (Fig. 1).

No variables that were tested significantly predicted the number of toots pair members produced during trials. Furthermore, age of the male was not a significant predictor in any model.

**Successful breeders from last season increased territorial behaviour during the breeding season**

Similar to results above, loons spent less time within 10 m of the decoy if they had breeding success last year ($F_{1,42}$=5.806, p<0.02) or had been exposed previously to the decoy ($F_{1,42}$=7.03, p<0.0113). Additionally, there

was an interaction between success last year and date of trial ($F_{1,42}$=4.916, p<0.0321), such that the date of trial correlated positively with time within 10 m of the decoy for loons that had success last year ($r^2$=0.357, $t_{22}$=3.5, p<0.002; Fig. 2). Loons without success the previous year showed no such correlation (p=0.65; Fig. 2).

A model using success within the last 2 years as a predictor variable did not significantly predict changes in behaviour over time.

**Other territorial behaviours**

In the current study, eleven males yodeled at least once at the decoy, and six males physically attacked the decoy during trials. The number of times males yodeled or physically attacked the decoy did not relate to breeding success, age, or pair territorial tenure.

# Discussion

This study is the first to our knowledge that links past breeding success to differences in territorial defence investment. Unexpectedly, we found that loons that successfully fledged chicks within the last 2 years responded less strongly to the decoy compared to loons that did not. This finding was contrary to our initial prediction based on the idea that animals invest in territorial defence in proportion to the value of territory; however, we also found that loons with breeding success in only the previous year increased their territorial response as the current breeding season progressed. Because successful loons experience higher rates of territorial intrusions (Piper et al., 2006), and a majority of territory usurpations occur on territories with recent chick production (Piper, Tischler, and Klich, 2000b), successful loons accrue higher costs in defending territory than unsuccessful loons. Our current findings suggest that successful loons adopt different territorial investment strategies than unsuccessful loons to offset the increased frequency of intrusions. One such strategy may be to limit investment in defensive behaviour (e.g., time spent attending to intruders) to the time of the season when it is most critical. For example, at the beginning of the season, successful owners may decrease territorial behaviour to build reserves lost during migration (Gray et al., 2014), and increase territoriality as the onset of mating and nesting approaches.

It is possible that there are intrinsic differences between successful or unsuccessful breeders, but our data also strongly indicate that previous breeding success causally alters territorial behaviour. For example, compared to loons that saw the decoy for the first time, loons that saw our decoy three years prior dampened their territorial responses, suggesting that both successful and unsuccessful loons remember past experiences and change their

territorial behaviour accordingly. Furthermore, our finding that successful loons increased territorial behaviours as the breeding season progressed was restricted to birds that were successful in only the most recent season (i.e., there was no such pattern for birds with success only two years before). If preexisting differences in territorial behaviour explained differences in breeding success, these differences should be consistent across years.

Previous data in loons (Jukkala and Piper, 2015), herons (Vennesland, 2009) and ducks (Forbes, Clark, Weatherhead, and Armstrong, 1994) are consistent with our finding that loons habituated to our decoy (for an exception, see Vennesland (2009)). However, these studies exposed animals to a decoy multiple times within a season and many studies use predator decoys instead of conspecific decoys. In the present study, no bird had seen the decoy for three years (Jukkala and Piper, 2015). This suggests that long-term recognition and memory of individual intruders is important for loons in allocating time and energy to territorial defence. In support of this interpretation, pre-breeding male loons prospect for breeding territories an average of 2.3 years in our study area, and intrude repeatedly on a subset of established territories during this time (Piper et al., 2015). However, a majority of evictions occur on lakes that the intruder has visited infrequently (Piper et al., 2015), which may indicate that owners benefit from increasing defencive behaviour to a novel intruder compared to one that has intruded before.

Finally, our finding that responses to the decoy decreased as the territory tenure of a pair increased may imply that stable pairs are more efficient at defending territory or that preexisting differences in territorial behaviour lead to differences in the lengths of partnerships. Future studies are needed to explore this relationship.

In conclusion, our data support the hypothesis that a loon's breeding history alters the perceived resource value of territory, and thus territorial behaviour. Results also reflect the possibility that preexisting differences in territorial behaviour lead to differential reproductive success.

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**Figure 1** (A) Loon pairs spent less time within 10 m of the decoy (measured in seconds) if the male loon had breeding success in either one of the past two breeding seasons, and if either pair member had been exposed to the decoy in a previous study. (B) The number of years loon pairs spent together on the current territory negatively related to time spent within 10 m of the decoy. Bar graphs represent means for each group $\pm$ SEM. * indicates $p<0.01$ for a main effect of success within the last 2 years and # indicates $p<0.01$ for a main effect of past exposure to the decoy.

**Figure 2** The time loon pairs spent within 10 m of the decoy (measured in seconds) during trials did not change as the breeding season progressed if (A) the male of the pair was unsuccessful at raising chicks the previous season, but increased as the season progressed if (B) the male of the pair had breeding success in the previous season.

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Figure Legends

Figure 1

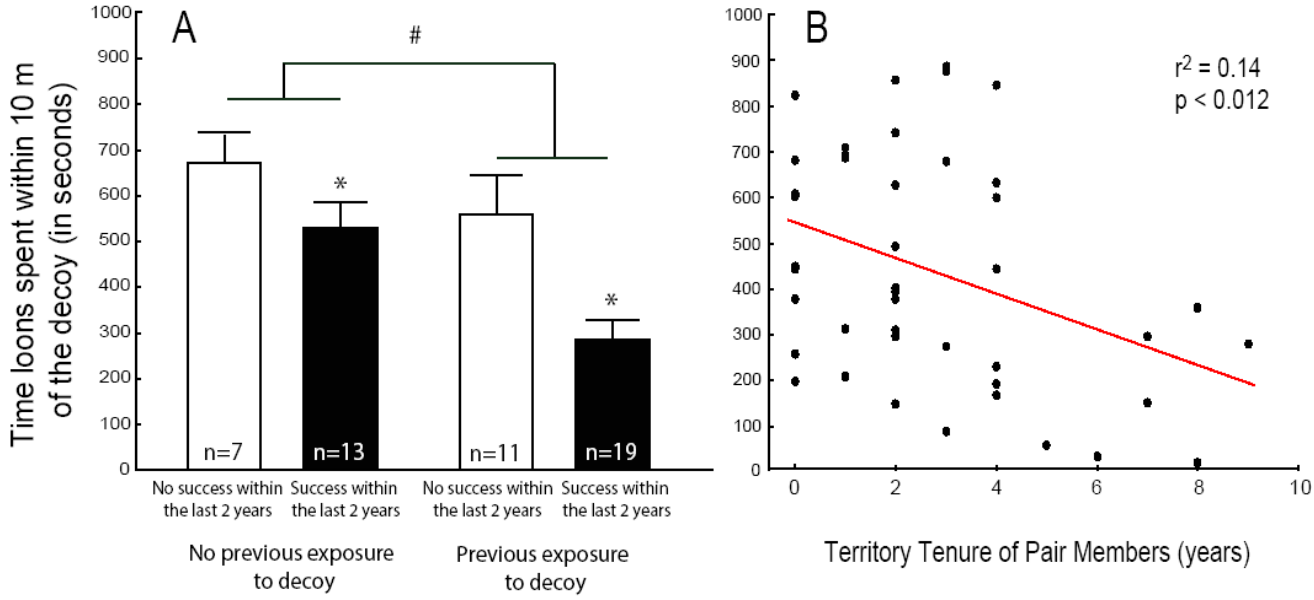

Figure 2