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Abstract

Animals that show aggression often risk injury and incur steep energetic costs. Thus, aggression should occur at such times and towards such opponents as to maximize fitness. We tested hypotheses predicting adaptive territorial aggression in the common loon, a species in which ease of observation of territory owners and floaters (prebreeders) seeking to evict them provide a rare window onto owner-floater competition. As predicted, older, more competitive floaters (4-year-olds and upwards) tended to intrude into territories that had produced chicks the previous year (and, hence, were of high quality). Older floaters also showed predicted increases in aggression and territorial yodeling, and a lower rate of submissive behaviors than younger floaters. Floaters of all ages intruded more often than neighboring territory owners, as predicted, but tended to avoid territories with chicks. For their part, owners yodeled more often and behaved more aggressively during chick-rearing, although yodels peaked in frequency two weeks before aggression, suggesting that males with young chicks yodel to discourage intrusions, but employ aggression to protect older chicks. Territory owners showed the predicted higher rates of aggression and yodeling towards older, more dangerous floaters than towards young, submissive ones. However, territorial pairs did not treat floaters more aggressively than neighbors, overall. Moreover, owners showed no spike in aggression nor yodeling following a year with chicks, perhaps to avoid providing social information to floaters that use chicks as social information to target territories for eviction.

Key words: territory, floater, social information, eviction, age, aggression

Significance Statement

Floaters are young nonbreeding individuals that compete with territory owners and are future breeders. Yet floaters are difficult to study because they are mostly unmarked, nomadic individuals. Owing to extensive efforts to capture juvenile common loons, we have established a large population of marked floaters in this species. Hence, loons offer a rare window to investigate efforts of floaters to settle on breeding territories. We found that older floaters (4 to 8 years), which are capable of evicting owners from their territories, target high quality territories for their intrusions, show more aggression, and show less submissiveness during intrusions than do young floaters. We further discovered that territory owners are more aggressive towards older, more dangerous floaters. Our findings show that territory owners recognize the degree of threat posed by each floater and treat each floater differently on that basis.

INTRODUCTION

Since aggressive behavior entails both risk of injury and high energetic cost, we would expect it to occur in such a way as to offer fitness benefits to the aggressor (Parker 1974). Aggression towards territorial intruders should be especially fine-tuned with respect to fitness. Territory defense, which is energetically expensive (Viblanc et al. 2016), must be balanced against the physiological costs of breeding as well as energy expenditures for courtship and rearing of offspring (Bales et al. 2000).

Two factors appear likely to explain most of the territorial aggression that animals show towards intruders. First, animals tend to behave aggressively at times when they are likely to gain fitness benefits from doing so, such as during a specific breeding stage (Briffa and Elwood

2001; Wright et al. 2019). Second, animals most often direct aggression towards specific intruders that represent the greatest threat to fitness (Hyman and Hughes 2006; Lehtonen and Wong 2017; Wright et al. 2019).

Floaters are important intruders in many territorial systems (Arcese 1989; Sergio et al. 2017). Defined as sexually mature individuals that live on the breeding grounds but have not yet settled on breeding territories, floaters can harm territory holders in numerous ways, including by reducing food levels (Penteriani et al. 2011), interfering with breeding (Sunde and Bølstad 2004), and even killing owners (Piper et al. 2008a; Newton 2010). Considering the fitness costs that floaters exact on territory owners, analysis of territorial behavior between owners and floaters is an obvious way to test predictions concerning the occurrence of aggression in territorial systems.

Although floaters constitute a crucial population cohort in territorial species, the nature of their relationship to territory owners is poorly understood for two reasons. First, floaters are often unmarked, because they are mostly young individuals that disperse from their natal area, wander widely (Moulton et al. 2013), and are difficult to capture (Laiolo et al. 2007). Consequently observers are often forced to learn about territorial aggression directed at unmarked floaters, whose ages, natal origins, and previous histories are wholly unknown (Walter 1990; Ryder and Sillett 2016). Second, floaters are often difficult to observe, because they live furtively amongst more conspicuous territory owners (Smith 1978; Rohner 1997; Penteriani et al. 2011).

Common loons (*Gavia immer*; hereafter "loons") are aquatic piscivorous birds that defend breeding territories on lakes from Alaska, across Canada and the northern United States, to Iceland. Loons breed in monogamous pairs, and are often visited by territorial intruders, which are either floaters or, less commonly, owners of nearby territories. Loons are especially suitable for a study of interactions between territory owners and floaters because: 1) they are large,

99 conspicuous, and vocal; 2) they occur in a habitat with few visual obstructions; 3) intrusions are
100 clustered, occurring mostly in July and during early morning hours; 4) all adult loons aggregate
101 during intrusions and seldom forage, which simplifies observation (Piper et al. 2006); and 5)
102 owners and floaters both pay more attention to conspecifics during intrusions than towards
103 humans, which allows observers to approach loons very closely at such times. Finally, floaters
104 never copulate with territory owners (Piper et al. 1997a), so floaters intrude to gain eventual
105 ownership of a territory, not parentage of young.
106 Beginning in 1993, we have investigated territorial behavior in a marked loon population in
107 northern Wisconsin. While some territorial intruders are owners from neighboring territories
108 (Piper et al. 1997b), most are floaters (Piper et al. 2015). Furthermore, floaters intrude into many
109 territories from ages two to eight years and claim territories from ages four to eight (Piper et al.
110 2006, 2015). Hence, loons offer an opportunity to test hypotheses concerning the timing of
111 territorial behavior and its dependency upon floater age.
112 Loons differ from many other solitary breeders in that floaters use the presence of chicks as
113 inadvertent social information ("ISI"; Danchin et al 2005) to assess the quality of specific
114 breeding territories (Piper et al. 2006). While conventional ISI is focused on entire habitats
115 where floaters prospect and settle without negatively impacting the conspecifics that produce the
116 social information (Doligez et al. 2002), a loon floater that detects young on a territory in one
117 year often returns to that territory the following year to evict its owner (Piper et al. 2000).
118 "Costly social information" forms the cornerstone of a territorial system in which loon parents
119 seeking to safeguard their territory tenure must hide their chicks from floaters (Piper et al. 2006).
120 (Killing of chicks by intruders is rare and only occurs when chicks are less than two weeks of
121 age (Jukkala and Piper 2015).) Parents attempt to achieve this objective in part through "dive and

122 scatter" behavior, wherein they dive and swim away from shore to draw intruders flying into
123 their territories to land near themselves, while their cryptic chicks dive and swim towards shore
124 to hide among rocks and logs (Piper et al. 2006).
125 We expected that floater territorial behavior during intrusions would be adaptive and reflect
126 age-dependent patterns in territory settlement. Our efforts were aided by previous study on the
127 species, which allowed us to place loon social behaviors along a continuum (Table S1) from
128 those showing: 1) submissiveness, 2) social interaction without aggression; 3) intense social
129 behavior likely to precede aggression; 4) overt aggression or escape from aggression; and 5) the
130 territorial yodel call.
131 To help focus our hypotheses, we classified two- and three-year-olds, which intrude into
132 breeding territories often but rarely settle on them (Piper et al. 2015), as young floaters and
133 floaters four-year and older, which settle routinely, as mature floaters (Piper et al. 2015). Our
134 predictions were as follows:
135 Prediction (1) Mature floaters, which have higher body mass and fighting ability than
136 young floaters and can thus compete with owners for territories and sometimes evict
137 them, should tend to visit high quality territories (i.e. those that had produced chicks
138 the previous year; see Piper et al. 2015) more often than low quality territories.
139 Young floaters, which are unable to claim territories, should show no such
140 preference.
141 Prediction (2) Mature floaters should engage in more territorial interactions, signal less
142 submissiveness, and show more aggression than young floaters, consistent with their
143 efforts to compete actively for territory ownership.

We further hypothesized that floaters as a group would show patterns of territorial intrusion aimed at territory settlement while territorial neighbors, which already possess territories, would not. This hypothesis led to four additional predictions:

Prediction (3) Floaters, which seek to learn about the presence of chicks, should make intrusions of longer duration than territorial neighbors.

Prediction (4) For the same reason, floaters should be more apt to approach owners and engage in more intense territorial interactions than neighbors.

Prediction (5) Floaters, which are weaker competitors than neighbors, should make fewer and shorter intrusions than neighbors into territories with chicks because those territories are likely to be defended vigorously.

Prediction (6) Floaters should show more territorial behavior in high-quality territories, which they might seek to claim from owners, than in low-quality ones.

Finally, we hypothesized that territory owners should behave adaptively with respect to defense of their chicks and territory and thus generated four final predictions:

Prediction (7) Owners should show frequent aggression and territorial yodels when their chicks are less than two weeks of age, because small chicks are sometimes killed by intruders (Jukkala and Piper 2015).

Prediction (8) Owners should exhibit vigorous territorial behavior in years following chick production, because it is during those years when intrusions and evictions are most frequent (Piper et al. 2000, 2006).

Prediction (9) Territory defense should be more vigorous towards floaters than neighbors, because only floaters pose a threat to territory ownership.

Prediction (10) Territory defense should be stronger towards more dangerous mature floaters than towards younger floaters (Piper et al. 2015).

METHODS

Study area and study animal

Since 1993, we have studied a marked population of common loons on a cluster of roughly 200 glacial lakes in northern Wisconsin, USA. Our study population comprises roughly 10% of all loons in the state. The study area, roughly 1700 km^2 in size, is centered at 45º42'N, 89º36'W, and covers central Oneida County and adjacent portions of Vilas and Lincoln counties. Lakes in this region are bordered by northern hardwood and coniferous forest, though most have highly developed shorelines and experience intensive boating, angling, and other recreational activity.

Loons in our breeding population winter in the Atlantic Ocean (chiefly on the Gulf Coast of Florida; see Kenow et al. 2021), and migrate to breeding territories in April, when lakes become ice-free. Incubation by both sexes lasts for 28 days; afterwards both sexes feed and protect their chicks on the water for up to eleven weeks. Territory defense ceases in September. Territories consist either of entire small lakes (0 to 200 ha; mean area $\pm$ SD: 56 $\pm$ 48 ha; 97 pairs) or protected sections of large lakes (> 200 ha; mean = 523 $\pm$ 448 ha; 12 pairs) that support multiple pairs.

Capture and field observation

Beginning in 1993, we have spotlighted adult loons and >90% of all chicks in our study area at night from a 4.3-m motorboat. Captured loons are brought to shore, given a USGS steel band and three colored plastic leg bands (Gravoglas 2-Plex: GravoTech, Inc., Duluth, GA, USA) for individual identification, weighed with a digital scale (Salter-Brecknell SA3N253; Fairmont, MN, USA), and released back into their territories in family groups.

Observers make visits of at least 1h to study territories once weekly from mid-May through early August. We did not explicitly design data collection so that observers record data blindly. However, observers are unaware of hypotheses, visit all study lakes on a rotating basis, and observe hundreds of marked loons with which they have little or no familiarity, rendering observer bias unlikely. On each visit, an observer locates and remains in a canoe within 20m of territory owners (such that they carry out normal behavior and ignore the observer); records all breeding activity, including presence of a nest or chicks; and documents nesting success or failure, if necessary, by inspecting nest contents (Piper et al. 2020). Observers identify all banded intruders from leg bands and record their arrival times, departure times, and all social interactions with territory owners and each other. While most pair members have been banded during the study, (e.g. 68% of 118, 86% of 174, and 81% of 218 individuals in 1999, 2009, and 2019, respectively), less than half of intruders have been banded during these three years (29%, N=340; 43%, N=887; 46%, N=333), chiefly owing to long-range natal dispersal by females into the study area (mean natal dispersal distances ± SD : males: 10.2 ± 7.0 km, N=128; females 32.1 ± 44 km, N=54). Nonetheless, we recorded intrusions by 279 different floaters of known sex (181 males; 98 females) that were initially banded as chicks during our study. We used these marked floaters for the analysis of floater behave that follows.

Determination of sex, age, and hatch date

We estimated a variety of variables used in our statistical analyses based on collected data. Sex was determined by: 1) the greater size of males (mean mass ± SD: 4,500 ± 310 g, $N = 1070$) than females (3,630 ± 250 g, $N = 914$) among territory owners; 2) observation of a yodel by a territory owner or intruder, which identified it as a male; 3) copulation within a breeding pair; or 4) genetic sexing of individuals banded as chicks (Itoh et al. 2001). Loons of unknown sex were excluded from analyses. We knew exact age only for loons banded as chicks on their natal territories; this group represented 2 of 118 (2%), 20 of 174 (11%), and 35 of 218 (16%) pair members in 1999, 2009, and 2019, respectively. Based on ages of settlement in such known-age adults, we estimated females newly banded as adults on territory to be seven years old and male settlers to be five years old (Piper et al. 2015). Hatch date for chicks was estimated by interpolation between the last date of incubation before hatch and the first date when a chick was observed.

Statistical analysis

In testing our hypotheses regarding owner and floater behavior, we used as dependent variables: 1) numbers of behaviors by territory owners or intruders, 2) numbers of intrusions by floaters or neighbors, or 3) duration of intrusions. To analyze the first two variables, which were counts, we employed negative binomial regression (model fit confirmed with the "countfit" command; Long and Freese 2014) in Stata 16.1 (StataCorp, College Station, TX, USA). We adjusted standard errors for repeated measures by using bird identity as a random effect.

Predictors examined for their statistical relationship with dependent variables included 1) chick age, 2) presence/absence of an active nest or chicks, 3) whether or not chicks were produced the previous year, 4) intruder type (floater or neighbor), and 5) age of floater. To improve model performance, we included covariates known to influence loon behavior from previous study: 1) number of intruders, 2) age of male owner, 3) year, 4) time of day, 5) duration of observation period, and 6) sex of intruder. After narrowing the list of predictors to those that addressed our hypotheses or were known to affect loon behavior from previous work, we carried out model selection by running all combinations of predictors and selecting the model that minimized Akaike's Information Criterion (AIC; see Burnham and Anderson 2002). We treated as nonsignificant predictors those whose addition to a model reduced AIC by less than 2 (Burnham and Anderson 2002).

RESULTS

Behavior of floaters that intruded

In support of our first two predictions, mature floaters behaved differently from young floaters both in the kinds of territories they visited and in their social behavior. In support of our first prediction, mature floaters (older than 4 years) were 25% more likely to intrude into territories that had produced chicks the previous year (Table 1), while young floaters were 21% less likely to do so (Table 2). Our second prediction was also strongly supported, as for each additional year of age, floaters were 17% less likely to show submissiveness to owners in the form of "initiates dive" behavior (Fig. 1; Table S2); 9% more likely to show intense territorial behavior in the form of simultaneous dives (Fig. 1; Table S3); 10% more likely to behave aggressively Fig. 1; Table S4) and 29% more likely to yodel (Fig. 1; Table S5).

Occurrence of intrusions and territorial behavior generally supported our hypothesis that floaters should be highly engaged in territorial interactions but should avoid high-intensity territory defense by owners. Consistent with our third prediction, floaters intruded for 4.4 minutes longer than neighbors, on average (Table 3; mean duration of intrusion ± SD: 33.5 ± 26.9 min, N=1251). In support of our fourth prediction, floaters showed a 35% higher probability of fleeing than neighbors, reflecting a tendency to approach owners closely and risk aggression from them (Table 4). Our fifth prediction too gained support: floaters were 17% less likely than neighbors to intrude into territories with nests or chicks (Table S6) and made intrusions that were 2.9 minutes shorter into territories with chicks than into territories without (Table 3). Our sixth prediction was supported in part, as social interaction by floaters increased on lakes that exhibited a previous year of chick production, including circle dances (↑ 26% greater likelihood; Table 5), simultaneous dives (↑ 47% likelihood; Table S3), bill dips (↑ 34% likelihood; Table S7), and initiates dives (↑ 40% likelihood; Table S2) but not aggression (↓ 2.7% likelihood; Table S4) or yodels (↓ 2.0% likelihood; Table S5).

Territorial behavior of owners

Territory owners showed territory defense at times and towards opponents in accordance with some, but not all of our predictions. In support of our seventh prediction, territory defense during the chick-rearing period was intense among pairs rearing small chicks. The likelihood of a yodel by the male parent peaked sharply at hatching and declined by 3% daily as chicks aged (Fig. 2; Table S8).

Aggression by territory owners also tended to decrease with chick age (by 1.1% per day; Table S9), but followed a different schedule from yodels, being infrequent at hatching, high when chicks were 2-3 weeks old, and low thereafter (Fig. 2). Contrary to our eighth prediction, yodels decreased in probability by 6% (Table S8) and aggression did not increase significantly (↑ 0.9% likelihood; Table S9) among pairs that had produced a chick or chicks the previous year. Our ninth prediction also was not supported. Territory owners were no more likely to yodel towards a floater than a neighbor (14% more likely to yodel at neighbors, a non-significant increase; Table S10) and did not exhibit significantly more aggression towards floaters than neighbors (8% increase in aggression towards floaters; Table S11). However, our tenth prediction was supported strongly: yodeling and aggression were both more likely towards mature floaters than young floaters (yodels: 11% increase in likelihood per year of floater age; Table 6; aggression: 15% increase in likelihood per year of floater age; Table 7).

DISCUSSION

While the loon territorial system exhibits some unusual features, like fatal contests (Piper et al. 2008a) and use of social information to target specific territories for eviction (Piper et al. 2006), it resembles those reported in other vertebrates in many respects. Loon floaters: 1) consist of both males and females, 2) visit established territories to compete for eventual territory ownership, and 3) neither forage nor seek extrapair matings during intrusions (e.g. Smith 1978; Schjorring et al. 1999; Bruinzeel and van de Pol 2004; Sergio et al. 2009a; Mayer et al. 2017) (Lardy et al. 2011). Therefore, our findings likely provide insights into the interactions of floaters and owners across many territorial animals.

304 We can now paint a detailed portrait of age-dependent behavioral strategies used by loon
305 floaters who seek to learn about and acquire territories. In short, two- and three-year old floaters
306 avoid high quality territories, behave submissively, seldom show aggression or yodel, and
307 generally appear bent on avoiding owner attacks until they mature and can compete for a
308 territory. However, even submissive young floaters likely use intrusions to collect information
309 about the presence of chicks (which indicates territory quality; Piper et al. 2006) and competitive
310 abilities of territory holders (Piper et al. 2015). This reconnaissance informs their efforts to
311 acquire high quality territories in subsequent years, as seen in other long-lived species
312 (Schjorring et al. 1999; Ferrer et al. 2015; Mayer et al. 2017; Barve et al. 2020). In contrast to
313 young floaters, four- to eight-year-olds more often visit high quality territories and exhibit a suite
314 of behaviors, including frequent simultaneous dives, aggression and yodeling, that indicate their
315 ability to compete for them.
316 The distinctive age-dependent behavior of young loon floaters finds parallels in other long-
317 lived species. For example, older, dominant Eurasian beavers (*Castor fiber*) intruding near their
318 home territories show a greater willingness to risk detection by territory owners than do young,
319 subordinate animals (Mayer et al. 2017). Likewise, young floaters in several species of long-
320 lived birds pose little immediate threat to territory owners, as in loons, yet collect information
321 about territory quality or improve in fighting ability over time in ways that facilitate later
322 eviction attempts (Zack and Stutchbury 1992; Ens et al. 1995; Bruinzeel and van de Pol 2004;
323 Sergio et al. 2009b; Ferrer et al. 2015). Hence, adaptive, age-related changes in aggressive and
324 settlement behavior of floaters are widespread in vertebrates.
325 An unusual aspect of our study is our pinpointing of conspicuous visual cues from intruding
326 loons that are likely to be used by owners to assess competitive ability and aggressive motivation

of floaters. Diagnostic behaviors of this kind are crucial elements of competitive behavior because they permit assessment of an opponent's fighting ability and thus allow contestants to invest appropriately in a contest (Enquist and Leimar 1983; Arnott and Elwood 2009). Yet visual signals that convey aggressive intent and competitive ability are more often presumed to exist than identified (Sergio et al. 2009b; Booksmythe et al. 2010; Nemesházi et al. 2018). Of course, many birds and anurans possess rich acoustic repertoires that include graded signals of aggressive intent (Wagner 1989; Owen and Gordon 2005; Searcy and Beecher 2009).

The conspicuousness of the territorial signaling system is a striking feature of common loon social behavior (Sjölander and Ågren 1972; Rummel and Goetzinger 1975). However, it remains uncertain whether loons truly signal their fighting ability and aggressive intent more clearly than other species, or whether the inherent difficulties of observing floater-owner interactions in most animals have simply limited the number of reports of such signaling. A rich system of graded signals might be expected in a species like the common loon that frequently engages in lethal battles, yet is long-lived and occurs in a habitat where unoccupied territories always exist (e.g. sequential assessment model; see Enquist and Leimar 1990). That is, when vacant territories are available nearby that offer territorial contestants other breeding options (Piper et al. 2008a), floaters and owners alike should benefit from the ability to gauge an opponent's strength and motivation to fight so that they can withdraw and settle elsewhere rather than committing to a costly contest.

Although floaters exhibited clear, adaptive patterns in territorial behavior overall, they showed two conflicting patterns when intruding into territories of high quality (i.e. those that produced chicks the previous year). On the one hand, their increased rate of non-aggressive social behaviors in high-quality territories suggests that floaters recognize their value. On the

other hand, floaters' lack of aggressiveness and yodeling in such territories, which parallels that of owners (see below), signals an unwillingness to escalate territorial contests for this valuable resource. It seems likely that floaters assess owners' fighting ability and motivation through low-cost social behaviors and engage in battles only in rare cases where they judge themselves capable of winning them, consistent with the sequential assessment model (Enquist and Leimar 1983).

In loons, floaters of both sexes compete vigorously for territory ownership and claim territories by evicting owners, as in many territorial animals (Freed 1986; Ens et al. 1995; Sergio et al. 2009b). Yet two obvious territorial behaviors differed between males and females, and these behaviors seem likely to be related. First, only males yodel, so only males can produce a signal of a heightened aggressive state (Mager III et al. 2012). The yodel would appear an adaptive cue that might allow both signaler and receiver to avoid a costly battle, since male loons frequently fight to the death, whereas females rarely do so (Piper et al. 2008a). Second, females flee more often than males during intrusions. Lacking an unambiguous signal of aggressiveness, female floaters probably must engage female owners closely to learn about their aggressive motivation. Such attempts at probing by female floaters are likely to trigger physical aggression in some instances, making it necessary for them to flee from the aggressor to avoid injury.

Territory owners are strongly affected by the obvious behavioral differences between young and mature floaters. Owners apparently use the social behavior of an intruder to gauge the level of threat it poses and to devise appropriate territorial responses. Aiming territorial behavior chiefly at mature floaters is likely to discourage repeat visits and eviction attempts by this dangerous cohort of intruders, while withholding aggression from relatively harmless young floaters saves energy and minimizes risk of injury. Aggression directed at dangerous opponents

373 is well-established in other territorial species, although more attention has focused on intruder
374 class (e.g. neighbor versus stranger; Temeles 1994; Christensen and Radford 2018) than intruder
375 age (but see Stutchbury and Robertson 1987). Efficient territory defense seems especially
376 important in loons, wherein owners seek to remain on a territory for many consecutive years
377 because of the benefits of familiarity (Piper et al. 2008b), yet must confront multiple intruders
378 each day (Piper et al. 2006).
379 In addition to targeting their aggression towards dangerous intruders, territory owners also
380 time their aggression and defense to maximize the benefits of these behaviors. Timing is
381 especially obvious in the case of chick defense. Like many other vertebrate species, loons use
382 aggression to keep conspecific intruders from injuring offspring during early life stages (Koskela
383 et al. 2000; Kober and Gaston 2003). Yodels peak in frequency at hatching. Hence, male parents
384 yodel: 1) to deter flying intruders from landing on the lake and 2) to prevent intruders already on
385 the lake from approaching just-hatched, highly vulnerable chicks (see also Jukkala and Piper
386 2015). Aggression by parents peaks three weeks later. Once chicks are three weeks old, they can
387 dive, swim to shore, and hide among rocks and logs, so they are less vulnerable to attack. Hence,
388 parents of older chicks permit intruders to land (as indicated by the lower rate of male yodels at
389 this stage) but behave aggressively when intruders are close at hand, likely as a means of
390 reducing the duration of intruder visits and thus hampering intruders' efforts to detect chicks and
391 use them as a cue for eviction attempts the following year. The infrequency and short duration of
392 floater visits into territories with chicks show the effectiveness of territorial yodels and
393 aggression together at limiting intrusions by floaters.
394 At first glance, it is puzzling that male loons with chicks do not yodel throughout the
395 chick-rearing period, since the yodel is a potent tool to keep intruders at bay. Consistent yodeling

could, in theory, serve the dual purposes of protecting chicks from occasional intruder attack and preventing intruders from spotting them (Piper et al. 2006). Yet males' tendency to yodel only in defense of small chicks implies that yodels have a cost and are not used except during times of critical need. The physiological cost of yodels is likely to be small, because they are emitted infrequently, unlike territorial calls of most songbirds. However, yodelers might pay a high social cost, because yodels betray information about identity, body size, and condition (Mager et al. 2007), likelihood of aggressive behavior (Mager et al. 2012), age (Piper et al. 2018), and probably also the presence of chicks, as suggested by our current findings. If floaters use the information encoded in a male's yodel to determine when to evict him, then the social cost of yodels explains their limited use.

Another curious finding of ours was the lack of increased territorial behavior by owners after a year of chick production (see also Spool et al. 2017). While owners might avoid increasing territory defense to recover from the energetic cost of rearing chicks the previous year, the carry-over cost from ten months prior is probably too small to explain this result. More plausible is that, again, aggression and yodels provide information that helps floaters bent on evicting territory owners. Specifically, yodels likely serve as social information that might reveal breeding success to floaters and thus help them target owners for eviction. If so, the lack of an increase in territory defense among territory owners with recent breeding success represents another attempt to withhold social information in order to safeguard long-term territory ownership.

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Author Contributions

WHP and KRL conceived of the analyses and analysed the data. WHP and BH contributed to field data collection. WHP wrote the manuscript with editorial suggestions from BH and KRL.

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Ethical approval

We followed all applicable international and national guidelines for the use of animals, and all procedures were approved by the Chapman University Animal Care and Use Committee (#2018-03). All techniques were non-invasive, and observers maintained a distance of at least 5 m from study animals.

Data availability

Data from this paper are accessible in the "Loon Project Database" at Chapman University Digital Commons (https://digitalcommons.chapman.edu/sees_data/3/) and also from Dryad (doi:10.5061/dryad.m905qftzf).

Conflict of interest

The authors declare no competing interests

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Figure captions

Fig. 1 Predicted numbers (± SEs) of six behaviors by floaters aged two to ten years during territorial intrusions. Values generated by random effects negative binomial models. Despite apparent declines in circle dances and bill dips after age seven, no overall decline emerged as important in our statistical models

Fig. 2 Probabilities of yodels and aggression by territory owners at different stages in the chick-rearing period from random effects negative binomial models