



## Territory settlement in common loons: no footholds but age and assessment are important



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Many animals face the task of locating and settling on a territory where they can produce offspring. Over the past 36 years, theoretical and empirical studies have provided growing support for the ‘foothold hypothesis’, which attempts to explain territorial settlement of long-lived animals. The hypothesis maintains that a young prebreeder lives within or intrudes into a cluster of breeding territories, accumulates site-dependent dominance there, then outcompetes other prebreeders for a territory within the cluster when it becomes available. We examined patterns in territorial intrusion and settlement among prebreeders of known age and natal origin to test the foothold hypothesis in the common loon, *Gavia immer*. We tested two other hypotheses for territory settlement: the maturation hypothesis, which posits that animals await physical and/or behavioural maturity before territory acquisition; and the assessment hypothesis, which maintains that prebreeders intrude into territories to assess fighting ability of territory owners, one of which they ultimately evict. We found no evidence for footholds in loons: prebreeders focused their intrusions within roughly 10 clustered territories, but intruded infrequently into the lake on which they later settled. Furthermore, prebreeders that waited years to usurp a territory had reproductive success no different from those that settled more rapidly on a vacant territory. The maturation hypothesis, in contrast, was supported in both sexes: prebreeders showed a sharp increase in fighting ability with age, and males exhibited age-related increases in mass and tendency to confront territory owners. The assessment hypothesis also gained support because intruders interacted extensively with owners and intruded frequently after territorial turnovers. Our study adds to a small but growing number of studies that fail to support the foothold hypothesis for territory settlement and support the conclusion that modes of territory acquisition might be more varied than previously thought. © 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Few events in an animal's life have such profound consequences as settlement in breeding habitat. At the settlement stage, an animal ceases wandering or dispersal and begins to focus its activity within a small breeding space, often a territory. Settlement has a dramatic impact on social behaviour, as settlers interact with a reduced set of conspecifics, chiefly their own mates and young and

neighbouring breeders. The move to a fixed breeding space has ecological impacts as well, because settlers become capable of consistent production of offspring.

Settlers are typically ‘floaters’, nonterritorial adults (Newton & Rothery, 2001; Tryon & Snyder, 1973) and often also ‘prebreeders’, floaters that have never held a territory. (Hereafter, ‘floater’ and ‘prebreeder’ will be used synonymously to refer to the latter group.) In recent years, advances in the theory of territory acquisition (Boulinier, Mariette, Doligez, & Danchin, 2008; van de Pol, Heg, & Weissing, 2007), together with studies of marked floaters during settlement (e.g. Bruinzeel & van de Pol, 2004;

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Sergio, Blas, & Hiraldo, 2009), have improved our understanding of floaters and the settlement process in long-lived animals (Penteriani, Ferrer, & Delgado, 2011). Although adult animals without breeding territories were once viewed as inferior competitors and the period prior to settlement a result of poor competitive ability (see Penteriani et al., 2011), researchers have come to regard the presettlement period, instead, as an opportunity for young floaters to improve the likelihood of settling where they will reproduce successfully (Boulinier, Danchin, Monnat, Doutrelant, & Cadiou, 1996; Smith, 1978; Stamps, Krishnan, & Reid, 2005; Zack & Stutchbury, 1992).

Among the most prevalent hypotheses for adaptive territory settlement by floaters is that of Smith (1978), who suggested that young rufous-collared sparrows, *Zonotrichia capensis*, lived furtively within several adjacent territories occupied by established owners and assumed positions within dominance hierarchies that could help them compete successfully for territory vacancies upon the death of a same-sex owner. Zack and Stutchbury (1992) built upon Smith's conceptual foundation, emphasizing 'reproductive delay' as an adaptive strategy to gain a high-quality territory. Their more general hypothesis maintains that a young animal settles on or near multiple high-quality territories, thus increasing its likelihood of occupying and defending one of them following an owner's death. Zack and Stutchbury pointed to an increase in competitive ability with age and site-dependent dominance of young floaters as factors that could promote this route to territory acquisition.

Many researchers have come to embrace the concept that young animals settle on or near high-quality territories to accumulate a competitive advantage in acquiring a territory in the event of an owner's disappearance. The concept has been termed the 'queue' hypothesis (Ens, Weissing, & Drent, 1995) and the 'site dominance' hypothesis (Sergio et al., 2009), but might be more aptly called the 'foothold' hypothesis (Piper, 2011), since animals can be said to gain a secure position in a specific area that makes it possible to improve their status there in the future. A large body of empirical evidence suggests that young animals might use footholds to acquire territories (Bruinzeel & van de Pol, 2004; Buston, 2004; Ens et al., 1995; Pärt, Arlt, Doligez, Low, & Qvarnström, 2011; Sergio et al., 2009; Wirtz, 1981).

Although it enjoys strong theoretical and empirical support, the foothold hypothesis is only one of several that aim to explain adaptive habitat settlement following a presettlement period. A second is the social information hypothesis, which maintains that young animals search for and later settle in habitats in which they detect conspecifics (Schmitt & Holbrook, 1996; Stamps, 1988) or evidence of successful conspecific reproduction (Doligez, Danchin, & Clobert, 2002; Reed, Boulinier, Danchin, & Oring, 1999; Valone, 2007). A third, the maturation hypothesis, suggests that an animal uses the presettlement period to hone foraging skills (Brandt, 1984), improve body condition (Sand, 1996; Weimerskirch, 1992) and increase fighting ability (Alvarez, 1993; Arcese, 1987) to the point where territory settlement and breeding are possible (Sergio et al., 2009; Weimerskirch, 1992). Finally, the assessment hypothesis (Arcese, 1987; Bruinzeel & van de Pol, 2004) posits that floaters intrude into territories to assess the fighting ability of the owner of their own sex and carry out territory usurpation (or eviction), a common mode of territory acquisition in many species (Calsbeek, Alonzo, Zamudio, & Sinervo, 2002; Ens, Safriel, & Harris, 1993; Packer & Pusey, 1983).

The common loon, *Gavia immer*, a migratory diving bird, provides a good opportunity to test hypotheses for territory settlement by floaters. Extensive banding of chicks in a study population in northern Wisconsin, U.S.A., has produced a large group of prebreeders of known age and natal origin that can be observed as they intrude into established territories (Piper, Grear, & Meyer, 2012; Piper et al., 2006).

Previous investigation has shown that the sexes settle by one of three means: (1) founding a territory in an unoccupied lake (38% of all settlements through 2014,  $N = 440$ ); (2) passive replacement of a breeder that has disappeared (26%); or (3) eviction of an established owner of the same sex following a battle (36%; Piper, Tischler, & Klich, 2000; Piper, Walcott, Mager, & Spilker, 2008a).

Since prior research has shown that loons use the presence of chicks as social information (inadvertent social information, sensu Danchin, Giraldeau, Valone, & Wagner, 2004) to target territories for intrusion (Piper et al., 2006) and usurpation (i.e. displacement of one pair member, followed by the pairing of its mate with the usurper, see Piper et al., 2000), we sought to test the remaining three hypotheses for habitat settlement: foothold, maturation and assessment. Although the three hypotheses are not mutually exclusive, each makes at least two unique predictions. The foothold hypothesis predicts that floaters should (1) reside within or intrude into a small cluster of focal territories as a means to gain site-dependent dominance in them (Smith, 1978; Table 2 in Zack & Stutchbury, 1992), (2) acquire a territory in which they have lived or intruded often (Zack & Stutchbury, 1992), (3) use a stable home range, so that site familiarity can accumulate (Zack & Stutchbury, 1992), and (4) gain a fitness payoff for waiting to settle (Smith, 1978). The maturation hypothesis predicts (1) improvement in body condition with age among young floaters, (2) increase in competitive ability with age and (3) a greater tendency to confront territory owners as resource-holding potential (Parker, 1974) improves with age (Cooper & Vitt, 1987). Finally, the assessment hypothesis predicts (1) frequent social interaction between intruders and territory owners, (2) frequent intrusions into territories with new owners and (3) a stable home range, since repeat intrusions into a territory could permit floaters to refine assessments of fighting ability by comparing social interactions with territory owners across intrusions (see Arcese, 1987, 1989).

## METHODS

### *Study Area and Study Species*

Territorial acquisition and defence by loons has been under investigation since 1993 in a roughly circular 800 km<sup>2</sup> area in north-central Wisconsin (centre: 45°42'N, 89°36'W) that contains a cluster of glacial lakes bordered by northern hardwood and conifer forest. Most lakes have highly developed shorelines and experience heavy recreational use. The species breeds in socially and genetically monogamous pairs (Piper et al., 1997), placing nests at the water's edge, often on islands, bogs or marshes (Piper, Walcott, Mager, & Spilker, 2008b). Males commonly produce a territorial call, the yodel, when intruders arrive, depart or fly over territories (Mager, Walcott, & Piper, 2007; Walcott, Mager, & Piper, 2006). As in most birds (Greenwood & Harvey, 1982), females disperse further from their natal lake to breed (mean distance  $\pm$  SD: 25.6  $\pm$  16.2 km;  $N = 35$ ) than males (10.3  $\pm$  6.5 km;  $N = 73$ ;  $t_{106} = 7.0$ ,  $P < 0.0001$ ).

### *Basic Field Procedures*

Beginning in 1991 we have spotlighted adult loons and their chicks at night during July and August, captured them in long-handled fishing nets, and fitted them with one U.S. Geological Survey metal band and three coloured UV-resistant plastic bands (Gravoglas 2-Plex: GravoTech, Inc., Duluth, GA, U.S.A.) in unique combinations (two bands per leg). At capture, each loon is weighed with a hanging scale (Electro-Samson SA3N253, Brecknell Scales, Fairmont, MN, U.S.A.). Starting in 2008, we have taken a drop of blood from each chick for sexing (amplifying a conserved region of

the W-linked EE0.6 segment and a Z-linked fragment as an internal control; see Itoh et al., 2001). Each adult or chick is released within 1 h in its territory. Capture, blood collection and observations are all carried out under permit from the U.S. Geological Survey and Wisconsin Department of Natural Resources and after approval from the Chapman University Institutional Review Board (no. 1112A126). Apparent annual survival is high among both adults (0.92; Grear et al., 2009) and chicks (0.77; Piper et al., 2012).

Measurements of mass were adjusted for the day of the year, because mass declines steadily in both males (5.0 g per day;  $t = -4.8$ ,  $N = 447$  males,  $P < 0.0001$ ) and females (3.4 g per day;  $t = -4.0$ ,  $N = 364$ ,  $P < 0.0005$ ) during the breeding season. To allow individuals caught on different dates to be compared, therefore, 5.0 g was added to male masses and 3.4 g to female masses for every day after 1 May that a loon was captured. The result was termed 'adjusted mass' and was used as an index of body condition (Brown & Sherry, 2006; Haramis, Nichols, Pollock, & Hines, 1986; Weimerskirch, 1992).

Crucial to the research has been attempted identification of loons from leg bands, which occurred on all encounters with individual loons or pairs. Loons' legs are usually submerged, but bands are often pulled out of the water and clearly visible during preening, head scratching, foot waggling (Paruk, 2009) and resting. In addition, most loons in the study area may be approached within 7 m without alarm, at which range bands can be seen underwater, if lighting is favourable. During territorial intrusions, owners and intruders are especially heedless of humans in canoes and may often be approached to within 2 m, if necessary, for identification. Partial or complete identification of loons is possible in flight, as legs are extended behind the body, allowing bands to be seen against a dark background.

From roughly 15 April to 9 May of each year (depending on date of ice-out), observers made scouting visits to 115 lakes routinely defended by breeding pairs as territories, which included 92 small to medium-sized lakes (mean size  $\pm$  SD:  $55 \pm 36$  ha) and 23 additional protected bays of 13 large lakes ( $303 \pm 297$  ha). During this interval, observers also scouted 82 small to medium lakes and nine parts of large lakes that loons were known to use and where they might have established territories. Each scouted lake or lake portion that lacked a territorial pair during the initial scouting period was visited again between 10 July and 10 August to check for the presence of loons and breeding activity. The list of lakes visited at least twice each year included all those within the study area that were greater than 24 ha (those likely to support loons; Evers, Paruk, McIntyre, & Barr, 2010), with the exception of two private lakes in the northwest corner (10 and 33 ha), where we were excluded by owners. Lakes or parts of lakes defended by pairs were placed on a list of all active territories, which comprised 90–100 each year.

Between 10 May and 10 August of each year, observers in canoes made routine 1 h visits (or longer, if necessary, to identify an intruder; mean  $\pm$  SD:  $66 \pm 11$  min;  $N = 662$  visits from 2014) every 4–6 days to each active territory to identify the resident male and female from leg bands using  $10 \times 40$  binoculars, determine the pair's reproductive status from nest-searching behaviour (Piper et al., 2008b), and check for presence of a nest or chicks. Visits were rotated with respect to both time of day and observer to limit bias.

#### Detection and Identification of Intruders

A key objective of each visit was to identify all intruders from leg bands. Intruders were easy for observers to detect, in general, because (1) they are large and occur in a habitat that lacks visual obstructions, (2) they can only intrude by flying into and landing conspicuously on territories that comprise entire small lakes (125

of 158 territories throughout the study period, 79%) and usually do so when intruding into large-lake territories, (3) pair members produce a 'toot' call when they see intruders flying overhead and (4) breeders assume an alert posture and usually approach when they spot intruders on the water (Piper et al., 2008b).

Although they were easy to see, we were not able to identify all intruders. In 2014, a typical year with respect to experience of the field team, 744 intruders were spotted. Of these, 64 (8.6%) were not observed well enough to determine whether they were banded (generally because they were departing from territories as observers arrived), but the legs of 680 (91.4%) were seen well enough to determine banding status. Of the sample whose legs were seen, 340 were positively identified as unbanded and 340 were positively identified as banded. Of the 340 banded intruders, 179 (52.6%) were positively identified as a specific banded individual.

Many chicks we banded in the study area returned there as adults. Through 2014, 232 of 566 (41%) chicks individually marked before 2011 had been seen in adult plumage as intruders, settlers or both. Of this sample, 222 (96%) intruded into territories at least once. Finally, of 99 individually identifiable floaters that settled on territories, 94 (95%) had been seen prior to settlement.

#### Statistical Analyses

Proper testing of many of our predictions relied upon detection of robust, unbiased samples of intruders and settlers. To investigate potential bias in the detection of intruders, we took number of intrusions as the dependent variable and as predictors we used (1) sex, (2) natal year and (3) centrality of intrusions (i.e. distance between the mean of coordinates of all lakes with intrusions and the geographical centre of the study area). Intrusions are counts; therefore we used a zero-truncated negative binomial regression ('`tnbreg`' command in STATA 12; StataCorp, College Station, TX, U.S.A.).

As a means of estimating the number of territories in a floater's home range, we regressed number of territories intruded upon on number of intrusions observed for all 140 intruders with at least two observed intrusions and analysed the fit of linear and nonlinear models with standard measures (heteroscedasticity and kurtosis). Since we were interested in predicting the precise relationship between the two variables, we sought a model that maximized  $R^2$ .

Mass data used to test the maturation hypothesis consisted of multiple recaptures of individuals, so we used repeated measures regression to analyse the change in mass with age ('`cluster`' option with '`regress`' command in STATA). The same technique was used to examine the relationship between straight-line distance between intrusions and time between intrusions, as most floaters were represented by two or more data points. Means are reported  $\pm$  SD, and all statistical tests are two tailed.

## RESULTS

#### Analysis of Bias in Intrusion and Settlement

Sex was not a significant predictor of the number of times that we identified a floater as an intruder ( $z = 1.4$ ,  $P = 0.15$ ), but more recent recruits ( $z = -4.3$ ,  $P < 0.0005$ ) and those that intruded far from the centre of the study area ( $z = -3.5$ ,  $P = 0.001$ ) had fewer observed intrusions than those that had more potential years of observation and those that intruded near the centre of the study area (pseudo  $R^2 = 0.045$ ;  $N = 142$ : 43 females and 99 males of known sex). Settlers and nonsettlers did not differ in either distance between intrusions (linear regression:  $t_{182} = 1.0$ ,  $P = 0.29$ ) or time interval between intrusions ( $t_{182} = 0.94$ ,  $P = 0.35$ ), but, again, settlers had intruded more centrally than nonsettlers ( $t_{262} = 2.9$ ,

$P = 0.002$ ). Among known-sex intruders, 67% of males ( $N = 89$ ) and 68% of females ( $N = 31$ ) were observed to settle.

### Reproductive Delay

Both sexes of loons appeared on the breeding ground in adult plumage years before settling (Fig. 1), a finding that supported this important assumption of the foothold, maturation and assessment hypotheses. In cross-sectional analysis, males were first observed in the study area at a mean age of  $3.4 \pm 1.2$  years ( $N = 78$ ) and settled at a mean age of  $5.9 \pm 1.6$  years ( $N = 51$ ), significantly later ( $t_{127} = 10.2$ ,  $P < 0.0001$ ). Females were observed at  $4.8 \pm 2.3$  years ( $N = 26$ ) and settled at  $7.4 \pm 2.1$  years ( $N = 24$ ;  $t_{48} = 4.2$ ,  $P < 0.0002$ ). Males both returned ( $t_{68} = 3.03$ ,  $P < 0.003$ ) and settled ( $t_{68} = 3.5$ ,  $P < 0.001$ ) at younger ages than females. A longitudinal analysis yielded similar results. Males were seen  $2.3 \pm 1.8$  years ( $N = 50$ ) and females  $2.6 \pm 2.7$  years before settlement ( $N = 20$ ).

### Tests of the Foothold Hypothesis

#### Prediction 1

The prediction that floaters should intrude into a small cluster of territories received qualified support. Floaters did tend to intrude into sets of territories that were clustered spatially; the mean distance between consecutive intrusions (7.0 km) was much shorter than the mean distance between lakes in the study area (19.0 km;  $t_{142} = 26$ ,  $P < 0.0001$ ; Fig. 2). As expected, floaters with more intrusions were observed in more different lakes (adjusted  $R^2 = 0.79$ ,  $N = 140$ ,  $P < 0.0001$ ), but heteroscedasticity was high and the fit poor for the linear model, owing to large residuals at large values for number of intrusions. In contrast, a model based on the logistic function ('nl' command with 'log3' function in STATA) provided a better fit (adjusted  $R^2 = 0.95$ ,  $N = 140$ ,  $P < 0.0001$ ). The logistic model placed a horizontal asymptote at 9.7, an estimate of the number of territories in a floater's home range.

#### Prediction 2

Contrary to prediction, floaters showed no tendency to settle where they had intruded often. Among settlers whose territory had been studied for at least 3 years prior to settlement ( $N = 37$ ), the group that settled on a preferred lake (i.e. one with as many

intrusions as or more intrusions than any other) actually displayed a significantly weaker preference than those that did not settle on a preferred lake ( $t_{35} = 2.2$ ,  $P = 0.04$ ). Within a narrower sample of 23 floaters that showed a clear preference for one lake (more intrusions there than on any other), only four later settled on that lake (assuming a home range of 10 territories, see Prediction 1; binomial test: mean = 4,  $N = 23$ ,  $P = 0.19$ ). Finally, among 324 intrusions by this group of settlers, only 30 (9.3%) were into the territories where they later settled (Fig. 3a, b, c), significantly fewer than expected assuming as frequent intrusion into the settlement territory as into other lakes with intrusions ( $t_{35} = -3.8$ ,  $P < 0.001$ ).

#### Prediction 3

The prediction that floaters would have stable home ranges received mixed support, as home ranges remained in the same general areas but drifted over time. As noted earlier (see Prediction 1), home ranges tended to occur in areas that were small compared to the entire study area, indicating stability in home range. Furthermore, the distance between the first intrusion lake and each subsequent lake was not related to the time interval between intrusions ( $F_{1,183} = 2.4$ ,  $N = 579$ ,  $P = 0.12$ ). However, among 81 floaters with three intrusions or more across 2 years or more, the distance between the first and last recorded intrusions was significantly greater than the mean distance between consecutive intrusions (paired  $t_{80} = 4.2$ ,  $P < 0.0001$ ), which revealed spatial drift.

#### Prediction 4

Our findings lent no support to the crucial prediction of increased reproductive fitness following reproductive delay (Fig. 4). Among floaters that usurped or passively replaced existing owners (and, hence, might have used footholds) and had been on the territory for at least 3 years, 137 of 252 (54.4%) produced chicks, whereas among founders, which used no footholds but instead settled in a vacant territory, 63 of 115 (54.8%) did so (Fisher's exact test:  $P > 0.99$ ; power to detect a difference of 20% = 0.94; Lentz, 2009). Usurpers and passive replacers also held onto their territories for no longer (mean  $3.4 \pm 3.2$  years) than founders ( $3.0 \pm 2.5$  years;  $t_{378} = 1.0$ ,  $P = 0.32$ ; power to detect a difference of 1 year = 0.90).

### Tests of the Maturation Hypothesis

#### Prediction 1

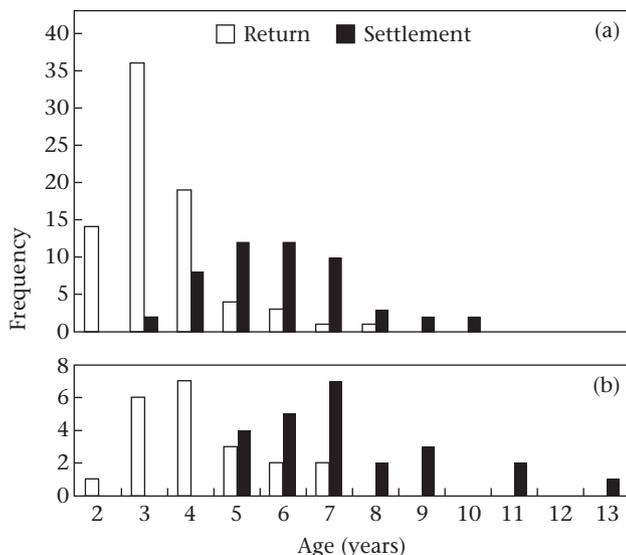
Consistent with the prediction of increased resource-holding potential with age, floaters of both sexes tended to found territories in vacant territories when young (i.e. 3–5 years in males; 5–6 years in females), but abruptly began to usurp established territories as they grew older (ages 5–6 years in males; 6–7 years in females). Usurpers were significantly older than founders in both males (Mann–Whitney test:  $U = 375$ ,  $N_1 = 18$ ,  $N_2 = 28$ ,  $P = 0.006$ ; Fig. 5) and females ( $U = 48.5$ ,  $N_1 = 7$ ,  $N_2 = 8$ ,  $P = 0.02$ ; Fig. 5).

#### Prediction 2

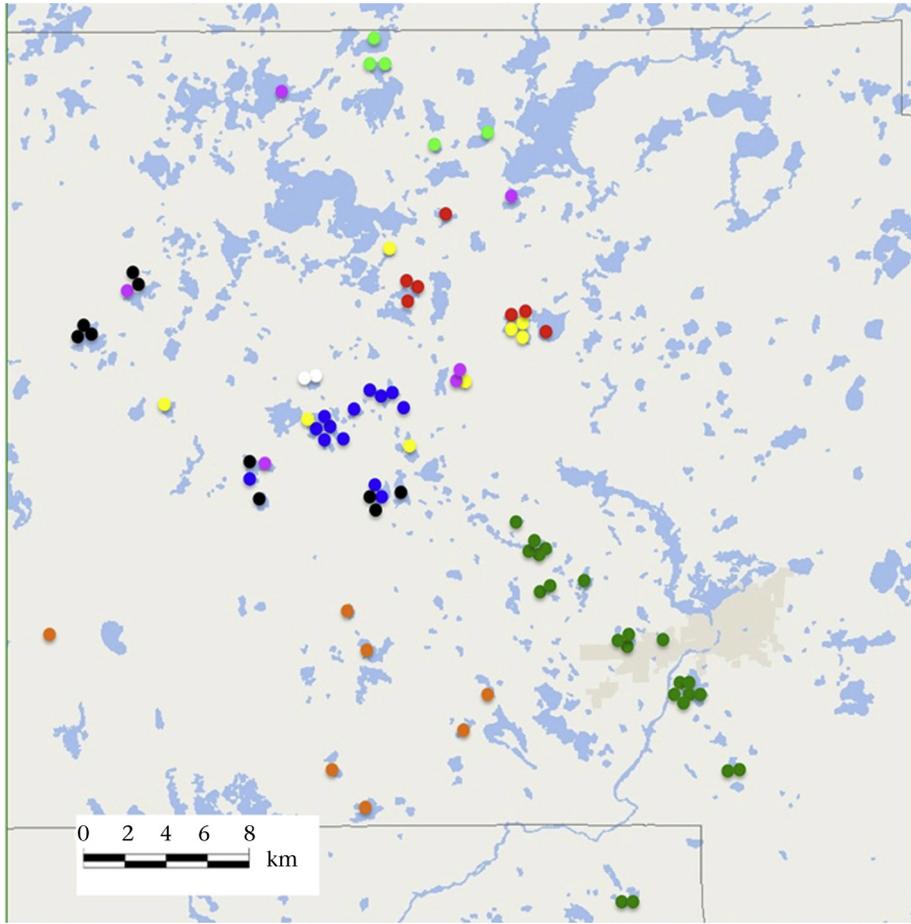
Consistent with prediction, body condition appeared to improve among young males of settlement age, as mass increased significantly during the period of territory settlement, 4–10 years of age (linear regression:  $F_{1,41} = 7.6$ ,  $N = 60$ ,  $P = 0.009$ ; Fig. 6). However, the pattern was absent in a smaller sample of females of settlement age (6–12 years;  $F_{1,15} = 0.22$ ,  $N = 23$ ,  $P = 0.65$ ).

#### Prediction 3

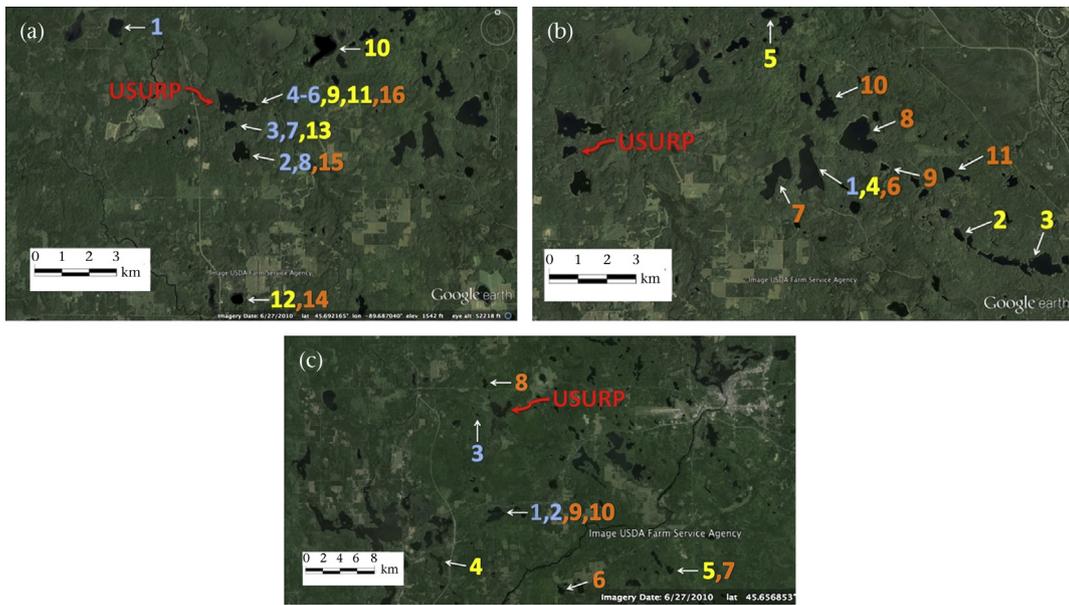
Based upon the apparent increase in resource-holding potential among young male floaters, this group should have intruded more often into territorial lakes from ages 2 to 10 years, as compared to



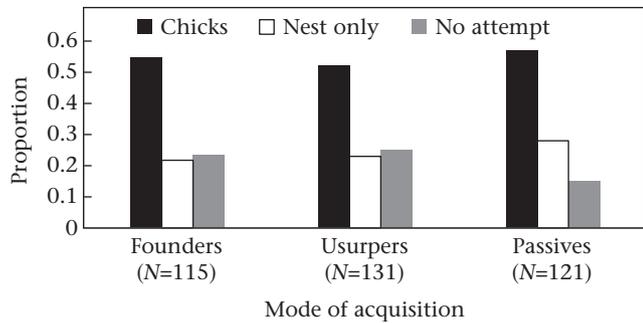
**Figure 1.** Distribution of ages at which (a) male and (b) female loons returned to the study area and settled.



**Figure 2.** Intrusion histories for eight randomly selected prebreeders (each a different colour) within the entire study area.



**Figure 3.** Intrusion histories for three floaters with 10 or more observed intrusions. (a) Occasional floaters showed a pattern of repeated intrusions into a small set of adjacent lakes followed by successful settlement in one of those lakes, a pattern predicted by the foothold hypothesis. (b, c) Typical floaters, however, intruded into many lakes and settled on a lake into which they had been seen to intrude seldom or not at all. Each colour indicates intrusions within a year (blue = first year; yellow = second year; orange = third year), numbers indicate chronology, and all prebreeders are different from those shown in Fig. 2.



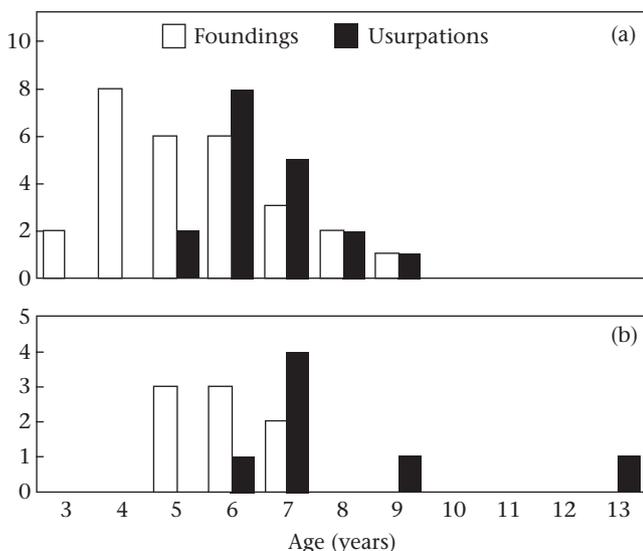
**Figure 4.** Proportions of floaters that hatched chicks, nested unsuccessfully or did not nest during their territorial tenure by mode of territory acquisition. Floaters gained territories either by founding, usurping or passively replacing a breeder that had disappeared.

visits to nonterritorial lakes. Indeed, tendency to intrude into defended territories increased with age class (linear regression:  $r = 0.69$ ,  $t_7 = 2.5$ ,  $P = 0.04$ ). Small samples prevented a parallel analysis in females.

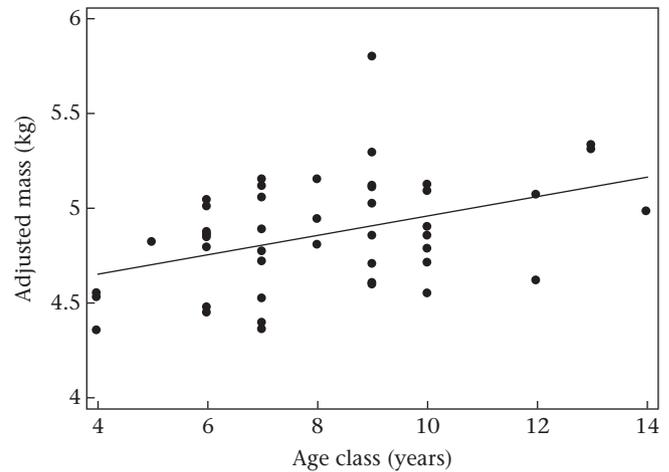
#### Additional Effects of Age and/or Experience

Founding and usurpation were not separate, fixed behavioural strategies used by two different sets of loons, but were instead alternative tactics within a single conditional strategy. This fact is clear from longitudinal analysis, because 10 males founded territories when young (mean age  $4.6 \pm 1.4$  years) and usurped territories when they grew older ( $7.4 \pm 1.5$  years). Two females did likewise: both founded at 7 years of age and usurped at 9 years of age.

Apparent changes in resource-holding potential appeared to occur later in life as well. Most loons that settled on a second breeding territory after having been evicted from a first one did so by founding, rather than by usurpation or passive replacement (Fig. 7). The rate of founding by evicted loons was far higher than the rate of founding among all other loons ( $\chi^2_2 = 23$ ,  $P < 0.0001$ ). Thus, loons displaced from their territories tended to resume a mode of nonaggressive territory settlement similar to that in very young adults.



**Figure 5.** Ages of (a) males and (b) females that claimed territories by founding (settling in a vacant area) or usurpation.



**Figure 6.** Adjusted mass versus age class for all captured male loons of known age and fitted line from linear regression.

#### Tests of the Assessment Hypothesis

##### Prediction 1

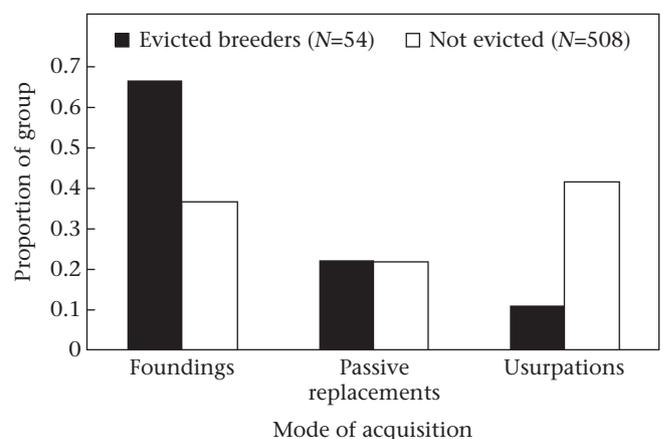
Floaters almost always interacted with territory owners during intrusions, a unique prediction of the assessment hypothesis. Of 227 cases in which marked floaters were observed as they flew in and landed in a defended territory, 222 times the floater approached and engaged in stereotyped social interactions with one or both territory owners (98%).

##### Prediction 2

A second unique prediction, increased intrusions into territories following a change in ownership, was also supported. Controlling for the strong impact of the previous year's chick production (Piper et al., 2006), intrusion rates were indeed higher in 30-day periods following turnovers (i.e. usurpations and passive replacements; 0.70 per h) than the identical 30-day period in the previous and subsequent year combined (0.52 per h; paired  $t_{153} = 2.4$ ,  $P = 0.02$ ).

##### Prediction 3

The prediction that floaters should intrude into a fixed set of territories gained partial support. Although floaters tended to



**Figure 7.** Proportions of loons that settled in a new territory by founding, passive replacement or usurpation, among those that had been evicted or not evicted from a previous territory.

intrude into territories in the same general area over time (foothold hypothesis, Prediction 1), they also tended to shift somewhat geographically in their intrusion patterns (foothold hypothesis, Prediction 3). However, floaters showed an additional tendency to make consecutive intrusions into the same territories over short time intervals, as revealed by high negative correlation between rate of repeat intrusions by a loon into a territory and the number of intrusions it had made since its first visit there ( $r_{23} = -0.50$ ,  $P = 0.01$ ). In summary, floaters shifted the locations of their intrusions over the years but remained within the same general area and exhibited short-term fidelity to certain territories.

## DISCUSSION

### *Lack of Bias among Intrusions and Settlements*

We detected no bias in number of intrusions between settlers and nonsettlers that was likely to affect the testing of predictions. Number of intrusions and detection of settlers were both related to centrality of a floater's home range; floaters that lived near the periphery of the study area made fewer intrusions and were less often detected as settlers, probably because they often intruded and settled in lakes outside the study area.

### *Territory Settlement in Common Loons*

Prebreeders did not appear to establish site-dependent dominance within a small home range to lay the groundwork for future territory ownership, as suggested by the foothold hypothesis. Instead, many prebreeders settled on vacant territories when young, at which point low resource-holding potential prevented them from competing successfully for existing territories. Others established home ranges containing about 10 territories, interacted extensively with owners, and claimed existing territories by usurpation or passive replacement when their competitive ability had increased. Surprisingly, usurped territories did not differ from founded ones in either chick production or duration of residency; thus, usurpers were apparently not repaid for reproductive delay by seizing high-quality territories. Once evicted from their own territory, most loons resumed the strategy of territory settlement that they had used as young prebreeders; that is, they founded a territory on an undefended lake. Hence resource-holding potential appears to be low early in a loon's life, high after a few years, and low again later in life.

The system of territory acquisition in loons bears a strong resemblance to that of male song sparrows, *Melospiza melodia*, which exhibit a rise in resource-holding potential early in life and a decline among older animals (Arcese, 1987). Like loons, song sparrows often usurp territories, rather than awaiting territory vacancies created by mortality. Finally, male floaters target vulnerable males for usurpation attempts (Arcese, 1987), consistent with the apparent assessment that occurs in loons.

### *Age and Reproductive Delay*

Young loons experienced a striking rise in competitive ability with age, an increase that co-occurred, in males, with a sharp increase in body mass. This result, together with the direct correlation between body mass and length of territorial tenure in loons (Piper et al., 2000), strongly suggests that greater mass is associated with increased fighting ability in this species. But the increase in competitive ability with age appeared to result merely from a general improvement in body condition (i.e. across all territories) and not an increase in site-dependent dominance owing to repeated intrusions within specific territories (Zack & Stutchbury,

1992). Age has a profound impact on resource-holding potential in many animals (Archie, Morrison, Foley, Moss, & Alberts, 2006; Jandt, Tibbetts, & Toth, 2014; Kitano, 1996; Sergio et al., 2009; Thavarajah, Fenkes, & Clutton-Brock, 2014). In some species, researchers have been able to pinpoint size, not age, as the true correlate (Bergeron, Grignolio, Apollonio, Shipley, & Festa-Bianchet, 2010; Elias, Kasumovic, Punzalan, Andrade, & Mason, 2008; Olsson & Shine, 1996). In either case, however, young of many species face a constraint, because they are unable to compete for breeding spaces effectively until they reach physical maturity.

The broad occurrence of age-dependent resource-holding potential in animals suggests that mere lack of physical or behavioural maturity is the most important cause of reproductive delay. If so, the strategy of using a foothold to acquire a breeding space is not a cause of reproductive delay, as suggested by Zack and Stutchbury (1992), but an adaptation to reduce its negative impact on fitness. The age constraint probably helps to explain other behaviours of young prebreeders that lead to adaptive habitat settlement, such as use of inadvertent social information. That is, lacking sufficient resource-holding potential to gain or hold a breeding space, young prebreeders can, none the less, increase future fitness by using the reproductive success of conspecifics as a cue to guide their eventual settlement (Danchin et al., 2004).

The pattern of age-dependent territory settlement seen in loons cannot be explained by residual reproductive value. The residual reproductive value hypothesis would predict a steady and consistent increase in resource-holding potential throughout life, because an animal should expend energy and assume risk in competitive interactions in inverse proportion to its expectation of future reproductive success (Grafen, 1987; Sergio et al., 2009; Shuttler & Weatherhead, 1992). Loons' resource-holding potential rises initially, as predicted by the hypothesis, but then falls, counter to expectation. Residual reproductive value remains a possible explanation for fatal fighting in old male loons, however, because this group may respond adaptively to declining expectation of future reproductive fitness in their final years by fighting dangerously (Piper et al., 2008a).

### *Why No Footholds in Loons?*

At first glance, the common loon would seem a likely candidate for footholds. Loons are long-lived (Evers et al., 2010), so it seemed plausible that they might invest time during the presettlement period to establish site-dependent dominance in high-quality territories. In addition, prebreeders intrude frequently into established territories, providing a potential avenue for footholds to develop (Piper et al., 2006).

Four factors seem to weigh against footholds in this species. First, prebreeders that intrude are spotted quickly by territory owners, and thus have less opportunity to develop site familiarity and site-dependent dominance than species that can intrude and display often (Heg, Ens, Van der Jeugd, & Bruinzeel, 2000) or live furtively within others' territories (Buston, 2004; Smith, 1978). Second, most loon populations appear not to show habitat saturation, owing to loons' high site fidelity and limited capacity to colonize new lakes (Evers et al., 2010). With many suitable territories available (e.g. Piper, Palmer, Banfield, & Meyer, 2013), prebreeders might often enjoy greater fitness by settling to breed when young rather than queuing for an existing territory. Third, territory quality is difficult to assess. No clear territorial feature demarcates territory quality in loons (as in other species, see Ens, Kersten, Brenninkmeijer, & Hulscher, 1992; Krebs, 1971), so prebreeders cannot identify territories likely to produce offspring by a quick inspection (although they do use chicks as an indication of this; Piper et al., 2006). Fourth, loons practise natal-habitat

imprinting (or NHPI: natal-habitat preference induction, Davis & Stamps, 2004), tending to settle on breeding lakes that resemble their natal lake in size and pH (Piper et al., 2013). Hence, young loons are not competing vigorously for specific high-quality territories, as seems to occur in other species (Johansson & Jonzén, 2012; Sirot & Touzalin, 2014; Smith, 1978; Zack & Stutchbury, 1992). Rather, each young loon seeks to found or usurp a territory on a breeding lake similar to its own natal lake.

Natal-habitat imprinting appears to pose a further challenge to establishment of footholds. If a loon seeks to settle on a natal-like territory, intrusions into a cluster of adjacent territories are unlikely to position it to do so, because features of lakes that loons use for natal-habitat matching exhibit no significant spatial autocorrelation. That is, adjacent lakes tend to differ greatly in size and pH (the features on which natal-habitat imprinting is based; Piper et al., 2013), so establishment of a home range in a cluster of adjacent lakes would not allow a prebreeder to establish site-dependent dominance within a set of natal-like lakes.

Two other well-studied species exhibit a clear lack of footholds and, thus, offer an instructive comparison to loons. In red-winged blackbirds, *Agelaius phoeniceus*, floaters show an ability to develop site-dependent dominance once settled on vacant territories (Beletsky & Orians, 1989), but they intrude into scores of territories while floating (Shutler & Weatherhead, 1994). This species can neither live within nor make lengthy intrusions into defended territories, because they are quickly detected and chased by territory owners (Peek, 1972). Lacking a means to accumulate site-dependent dominance, like loons, and also the capacity to evict owners (Shutler & Weatherhead, 1994), red-winged blackbirds simply intrude into large numbers of territories, eventually finding a vacant one to claim. Floaters in the black kite, *Milvus migrans*, are able to accumulate site-dependent dominance on a territory (Sergio, Blas, Forero, Donazar, & Hiraldo, 2007). Hence, the territorial system might appear to support the establishment of footholds. But in this migratory species, floaters use home ranges that broadly overlap hundreds of defended territories (Tanferna, López-Jiménez, Blas, Hiraldo, & Sergio, 2013) and evidently dedicate their time not to gaining footholds but to learning about territory quality (Sergio & Penteriani, 2005), so that they can seize a good territory through 'pre-emption' (spring arrival before the owner from the previous year; see Sergio et al., 2007; Sergio et al., 2009).

#### *How Prevalent are Footholds in Territorial Species?*

A partial review among birds over two decades ago suggested that young floaters of many species use ranges encompassing only two to six territories (see Table 2 in Zack & Stutchbury, 1992), suggesting that footholds might be widespread in territorial animals. But recent studies have reported home ranges that far exceed this size (Shutler & Weatherhead, 1992; Tanferna et al., 2013) and that, therefore, cannot support footholds. Our findings indicate that even prebreeders that intrude into relatively few territories might not use footholds. Thus, it is becoming apparent that footholds are only one means by which prebreeders might position themselves for future territorial ownership.

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