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Can settlement in natal-like habitat explain maladaptive habitat selection?

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The study of habitat selection has long been influenced by the ideal free model, which maintains that young adults settle in habitat according to its inherent quality and the density of conspecifics within it. The model has gained support in recent years from the finding that conspecifics produce cues inadvertently that help prebreeders locate good habitat. Yet abundant evidence shows that animals often fail to occupy habitats that ecologists have identified as those of highest quality, leading to the conclusion that young animals settle on breeding spaces by means not widely understood. Here, we report that a phenomenon virtually unknown in nature, natal habitat preference induction (NHPI), is a strong predictor of territory settlement in both male and female common loons (*Gavia immer*). NHPI causes young animals to settle on natal-like breeding spaces, but not necessarily those that maximize reproductive success. If widespread, NHPI might explain apparently maladaptive habitat settlement.

1. Introduction

An animal's settlement in breeding habitat represents a crucial step in its life history. At this stage in most species, an individual ceases a roaming existence and becomes capable of systematic production of offspring. Hence, the study of breeding habitat selection is of interest to a broad swath of ecologists, including those who study its relevance to populations and those concerned with the means by which an animal learns about and acquires breeding space. Habitat selection has taken on greater importance in recent decades, as humans have reduced the quality and quantity of habitat available to most animals, exotic species have invaded many regions, and breeding ranges have shifted owing to climate change [1].

Historically, a major conceptual foundation for understanding habitat selection has been provided by the ideal free and ideal despotic models [2]. The ideal free model posits that animals settle in a habitat according to its quality and the density of conspecifics within it, leading to equal fitness for all settlers. The ideal despotic model assumes that some individuals exclude others from breeding spaces, which results in unequal fitness across habitats [2]. While these simple, intuitive models predict habitat settlement accurately in some cases and continue to be widely applied to natural populations [3,4], their restrictive assumptions, especially that of perfect information, have caused many workers to view them chiefly as heuristic tools [5,6].

An important recent advance in habitat selection theory is the realization that many animals find breeding spaces through 'social information', which may be intentional signals from conspecifics or, more often, inadvertent social information (ISI) that conspecifics produce in the course of biological activities [7,8]. Cues that indicate reproductive activity or success are a widespread and potent form of ISI; non-breeders that detect such cues in a certain area of breeding habitat tend to recruit to that area [9–11]. Indeed, use of ISI to locate breeding habitat has often been proposed as a remedy for the ideal models' problematic assumption that settlers have perfect information about habitats [4,10,12].

Despite recent progress in understanding habitat selection, workers remain baffled by the frequent failure of animals to settle in high-quality habitats [13]. Many species show a consistent tendency to overuse poor habitats [14–16], or recruit inefficiently [16–18] or not at all [6] to good ones. Together, these findings suggest that mechanisms of habitat selection as yet poorly known might cause animals to settle in habitats that do not maximize reproductive success [13,14,19].

One mechanism that might cause a mismatch between settlement preference and reproductive fitness is natal habitat preference induction (NHPI), a behaviour pattern by which animals encounter specific environmental cues in their natal site and settle as adults in breeding habitat that exhibits those cues [20,21]. NHPI has been described commonly in the laboratory, especially in insects (see review in [20]), but its ecological and behavioural ramifications have been little discussed until recently [21,22]. According to developing theory, NHPI could serve as an adaptive means of habitat settlement if it allows a young animal to (i) learn cues related to fitness and then search efficiently for a breeding space that exhibits those cues [20,23], or (ii) settle in a breeding space that suits its phenotype or skills it learned on the natal site [20,24,25]. A paucity of examples in free-living animals has limited the impact of NHPI on habitat selection theory. Evidence for NHPI to date comprises a handful of suggestive cases derived from genetic and behavioural data, but only one clear demonstration: a sample of 18 mice (*Peromyscus boylii*) that settled in either woodland or chaparral, in accordance with natal habitat type [26].

If common in nature, NHPI would appear a plausible explanation for the apparent failure of animals to occupy habitats of highest quality. Animals are thought to settle in natal-like habitat because it offers a suite of ecological challenges (such as distinctive foods or predators) with which they have become familiar during the juvenile phase, or because their phenotypes, which promoted survival in the natal site, do likewise at a natal-like site [20,21]. Therefore, use of NHPI for habitat settlement might not result in short-term reproductive success, which is the most common measure of habitat quality [1,5,13]. NHPI might be particularly useful to animals in variable environments, as it could provide a means for them to locate favourable, natal-like habitat from among many potential options.

We looked for evidence of NHPI in a population of common loons (*Gavia immer*) under study since 1993. Loons are appropriate for an investigation of NHPI for three reasons. First, survival rate of chicks to adulthood is about 50 per cent, and natal dispersal occurs over short enough distances that one can accumulate a large sample banded as chicks that settle within the study area [27] (figure 1). Second, loons defend territories that comprise entire small lakes, whose physical, chemical and biotic properties are monitored by a state wildlife agency as a means to safeguard fish populations for recreational angling. Third, non-breeders use the presence of chicks in a territory as ISI and to target territories for intrusion and takeover, a strategy that increases reproductive success [28]. Hence, loons offer an opportunity to compare the impact of NHPI with that of a well-known mechanism for habitat selection. We inferred the occurrence of NHPI from similarity between natal and settlement lakes, since we were unable to examine the process of territory settlement or measure territory preference directly.

2. Material and methods

(a) Study site and natural history of loons

Our main study area is a roughly 800 km² region in Oneida County, Wisconsin, USA (45°42' N, 89°36' W), containing a concentration of glacial lakes, each surrounded by northern hardwood and conifer forest. Additional observations come from a secondary study area of roughly 4000 km² in Vilas, Iron and Forest counties, which abut the main study area to the north, and from chance sightings of marked birds on territories 69 km north and 116 km south of the main study area.

Territories consist of entire small lakes (6–119 ha; $n = 90$) or, less commonly, protected bays (50–100 ha) in large lakes (175–1401 ha; $n = 24$). Loons nest chiefly on islands, bogs or marshes [29]; sexes jointly incubate the two-egg clutch and rear 1–2 chicks. Chicks and adults consume mainly fish, especially bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*) and brown bullhead (*Ameiurus nebulosus*), although tadpoles (family Ranidae), crayfish (*Orconectes virilis* and the invasive *O. rusticus*), leeches (subclass Hirudinea; *Nepheleopsis obscura*), snails (class Gastropoda; mainly the invasive *Bellamya chinensis*) and insect larvae (mostly dragonflies, order Odonata) are frequent prey. The semiprecocial chicks are initially fed small items by their parents, especially minnows (Cyprinidae), leeches and insect larvae. Chicks capture half of their own food by eight weeks and almost all by week 11 [29]. Families drift apart as chicks mature; adults and chicks migrate separately in November, chicks often departing shortly before lake surfaces freeze [29].

Ninety-two per cent of established owners survive to the next year [30], while 89 per cent return to their breeding territory of the previous year [31]. Hence, desertion of a breeding territory by either sex is rare, even in the event of repeated nesting failure [32]. If both pair members return, they take possession of the territory as soon as an ice-free portion of it permits them to land (usually in mid-April). If one member does not return, a male or female non-breeder typically fills the vacancy within a few days. Among non-breeders, prebreeders appear to arrive slightly later than do former breeders, as prebreeders are less numerous among territorial intruders in April and May (Pearson $\chi^2 = 14.5$, d.f. = 4, $p = 0.006$).

Territory acquisition occurs by three means: (i) passive replacement of a missing owner (122 of 453 acquisitions; 26.9%), (ii) usurpation of an existing territory from an owner ($n = 175$; 38.6%) or (iii) founding of a new territory on an unused lake ($n = 156$, 34.4% [32]). Based on a sample of 72 lakes covered for 13 years or more, only 88 per cent ($\pm 3\%$ s.d.) of all breeding lakes are occupied each year, so vacant lakes are always available where non-breeders could settle.

(b) Marking and observation of loons

Systematic capture of loons in the main and secondary study areas began in 1991. Adults and chicks 5 weeks or older were netted by spotlighting from small motorboats, and fitted with a single US Fish and Wildlife Service metal band and three-coloured plastic leg bands in unique combination (two bands per leg; Gravoglas 2-Plex; GravoTech, Duluth, GA). After marking, birds were released in family units within their territories.

To find chicks that had returned as adults to claim breeding territories at 4–11 years of age, we identified all colour-banded pairs in the main study area once each week between 25 April and 7 August from 1993 to 2012, and in the secondary study area once annually in April or May. Individuals were considered to have settled on a breeding territory if they remained there for at least 60 days with a mate and/or produced a nest with eggs there. Of 102 birds in this group, 87 (85%) nested and 66 (65%) produced chicks. While we focused chiefly on the single breeding lake where a loon first settled, 22 of 102 loons settled first on one lake and later on another, because of eviction or

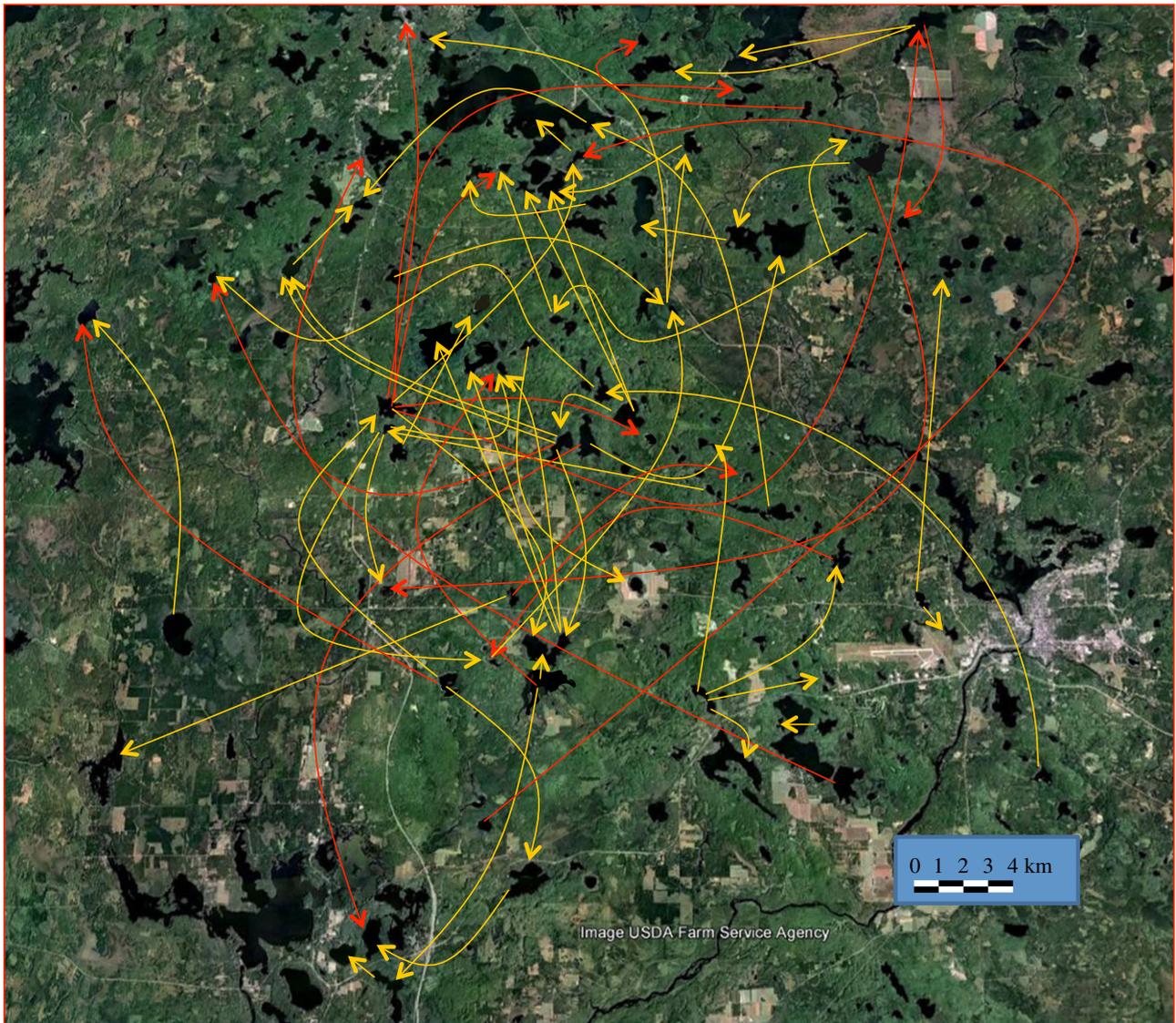


Figure 1. Natal dispersals of all males (yellow) and females (red) that both hatched and settled to breed in the main study area. Arrows point from natal to breeding lake. Not shown are 27 long-range dispersers that either hatched outside the main study area but settled within it ($n = 6$), hatched within the study area and settled outside it ($n = 11$), or both hatched and settled outside it ($n = 10$).

abandonment of their first territory [32]. Thus, we had the opportunity to examine the persistence of NHPI on second territories.

(c) Quantifying habitat

Study lakes vary in many respects, including morphometry (e.g. size, shape, depth), water source (seepage, drainage or spring), shoreline habitat (bog or upland), benthic composition (sand, rock or muck), water chemistry (pH and alkalinity) and biotic communities. However, we tested for NHPI only attributes that (i) were measured quantitatively, (ii) were available for all lakes, (iii) yielded consistent values across years, and, above all, (iv) exhibited substantial inter-lake variability. Six variables satisfied these requirements: lake size (using a 200 ha cut-off, equivalent to a maximum territory size; log-transformed to normalize), shape, maximum depth, water clarity (indicated by Secchi disk), pH and alkalinity. Shape, computed as perimeter divided by the square root of area, was a measure of where a lake fell on a scale from perfectly circular to highly convoluted.

(d) Test for spatial autocorrelation

Spatial autocorrelation is a common feature of habitats [33] and creates a potential problem for analysis of habitat use by animals.

If spatial autocorrelation is high, then animals that exhibit short-distance natal dispersal will tend to settle to breed in spaces similar to their natal spaces by virtue of spatial autocorrelation alone. So, in order to demonstrate that a result reflects active selection of habitat by animals (i.e. NHPI) and not merely spatial autocorrelation of habitat, one must show that natal dispersal occurs at a scale that is well beyond that of spatial autocorrelation [26].

The danger that spatial autocorrelation would confound NHPI seems less acute in loons than in the mammalian species examined to date [26,34]. Adjacent lakes in our study area tend to differ starkly in physical and chemical attributes, suggesting limited spatial autocorrelation. Moreover, natal dispersal typically carries male ($12.6 \text{ km} \pm 16.1 \text{ s.d.}$, $n = 67$) and female loons (25.8 ± 16.8 , $n = 29$) many territories away from their natal lake, and rarely to the adjacent one to breed (six of 102 settlements; 6%). No loon has ever settled in its natal territory (figure 1). Nonetheless, we examined all six attributes for spatial autocorrelation [33], using 68 nesting lakes that fell within a 12 by 28 km rectangular area (bounded by 45.60° N to 45.85° N latitude on S and N sides, -89.53° and -89.68° W longitude on E and W sides) in the centre of the study area [33] and for which data were complete.

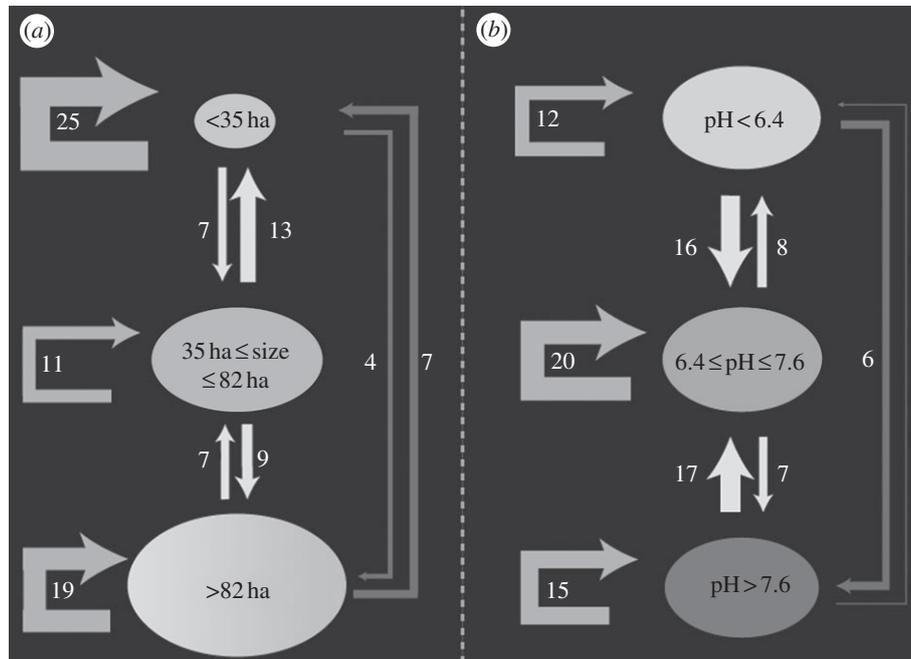


Figure 2. Settlements on breeding lakes of 102 young loons by size (a) and pH (b) of natal lakes. Lakes are broken down into three classes of equal size with respect to both size and pH. Numbers beside arrows indicate loons from natal lakes of each size or pH class that settled as adults in a lake of the same or different size or pH class. Widths of arrows are proportional to the number of settlements.

(e) Statistical analysis of natal habitat preference induction

Lake attributes that exhibited no evidence of spatial autocorrelation were analysed, within individuals, for similarity between natal and first settlement lakes. In order to test similarity and not merely correlation, we used a randomization procedure that tested the prediction that a loon's natal and first settlement lakes should differ by a smaller amount than lakes chosen at random within the sample. The procedure also accounted for non-independence of observations that came about since multiple loons were reared on the same natal lake and multiple others settled on the same lake. Each of 10 000 randomizations consisted of 102 random pairings (with replacement) of natal and first settlement lakes from which a mean difference was computed for each lake attribute. We computed two-tailed p -values by comparing the position of the empirical mean difference between natal and first settlement lakes for all 102 loons to the expected distribution.

3. Results

(a) Natal habitat preference induction in lake size and pH

Of six initial lake attributes examined, alkalinity was found to exhibit minor but marginally significant spatial autocorrelation and was dropped from the analysis (see the electronic supplementary material, figure S1). Thereafter, we continued with the remaining five variables.

Natal and first settlement lakes were more similar than expected when differences between them were computed for all five variables simultaneously by means of Euclidean distance (ED) and compared with Monte Carlo randomizations (ED = 2.47, mean of randomizations = 2.87, $p < 0.0001$). Natal and settlement lakes were especially similar in both size and pH ($p < 0.0001$ for both variables; sample mean compared

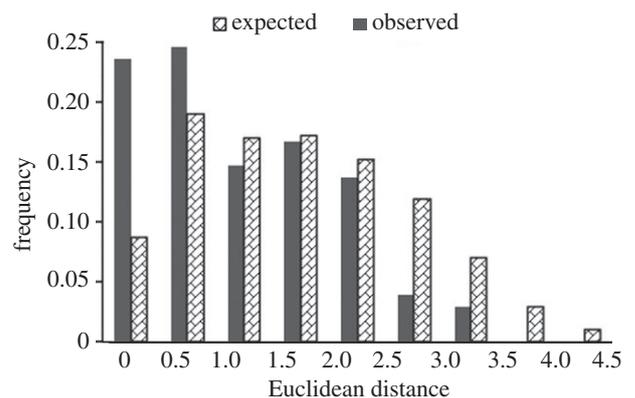


Figure 3. Observed and expected distributions of Euclidean distance between natal lake size/pH and first settlement lake size/pH. The greater proportion of individuals observed with very small Euclidean distances indicates NHPI.

with randomizations; electronic supplementary material, figure S2). In contrast, shape ($p = 0.028$), maximum depth ($p = 0.15$) and clarity ($p = 0.08$) did not differ significantly from expected based on an α of $0.05/5 = 0.01$ (Bonferroni-adjusted for five tested variables [35]). The statistical significance of lake size and pH resulted from the greater tendency of young loons to settle on breeding lakes that were either very similar to their natal lakes or moderately so, and to avoid lakes that differed greatly (figure 2). Since lake size and pH are moderately correlated ($R^2 = 0.34$, $p < 0.0001$, $n = 379$), we calculated residuals for lake size while controlling pH, and vice versa. Residual analysis confirmed that lake size ($p < 0.0001$) and pH ($p < 0.0001$) each contributed uniquely to NHPI (see the electronic supplementary material, figure S2).

We standardized values of lake size and pH, and collapsed them into a single measure of NHPI using ED. By producing a single measure, we were able to estimate the proportion of loons in the population that used NHPI (figure 3) and examine its consistency across contexts.

(b) Robustness of natal habitat preference induction

If spatial autocorrelation, not NHPI, accounted for the similarity between natal and breeding lakes, then loons that dispersed short distances should have exhibited low ED values compared with those dispersing longer distances. However, there was no evidence that ED was correlated with distance of natal dispersal ($r = 0.05$, d.f. = 100, $p = 0.31$, one-tailed), nor did mean ED for the shorter half of dispersal distances (1.23, s.d. = 0.85, $n = 51$) differ from mean ED for the longer half (1.24, s.d. = 0.80, $n = 51$; $t = 0.05$, d.f. = 100, $p = 0.48$, one-tailed).

Both sexes exhibited NHPI. Mean ED values for males (1.20 units; $t = 4.94$, d.f. = 66, $p = 0.0001$) and females (1.34; $t = 2.67$, d.f. = 30, $p = 0.0121$; four birds of unknown sex excluded) were significantly lower than the expected value (1.73) based on randomizations.

NHPI occurred in two of three modes of territory acquisition. Breeding territories were more similar to natal lakes than expected (ED = 1.73) when usurped (1.32 units; $t = 2.25$, d.f. = 23, $p = 0.034$) and founded (1.10 units; $t = 5.96$, d.f. = 31, $p < 0.0001$), while territories settled by passive replacement (1.56 units; $t = 0.64$, d.f. = 9, $p = 0.54$) were not, although a small sample makes the last test inconclusive.

(c) Natal habitat preference induction versus inadvertent social information indicating reproductive success

NHPI occurred both among territories that had produced chicks the previous year (mean difference in ED: 1.25 units, $t = 2.87$, d.f. = 22, $p = 0.0088$) and those that had not (mean: 1.26, $t = 4.52$, d.f. = 58, $p < 0.0001$). Hence, NHPI and ISI as chicks might exert independent effects on habitat selection. In other words, a natal-like lake is attractive, a lake with chicks is attractive, and a lake with both attributes is doubly so.

Although a direct quantitative comparison is impossible owing to non-overlap of samples, we can produce a crude estimate of the relative strengths of NHPI and ISI as chicks. In contrast to NHPI, ISI as chicks occurs in only one of three modes of territory settlement: usurpation. The 34.4 per cent of territories settled by founding cannot involve ISI as chicks, as they were vacant in the year before settlement. Similarly, ISI as chicks did not appear to be important in replacements of dead territory owners (26.9% of settlements), as the rate of such replacements following chick production (61 of 122, 50%) was indistinguishable from the mean rate of chick production across the population (553 chick-years out of 1092 total breeding-years, 51%; Fisher's exact test; $p = 0.92$). Thus, ISI as chicks can only have been important in the 38.6 per cent of loons that usurped territories. Usurpations were significantly more frequent in post-chick territories than expected (90 of 121 among all usurpers; 74.4%; 25 of 36 among prebreeders, 69.4%), based on the number of loon-years throughout the study (1015 of 1641; 61.9%; Pearson $\chi^2 = 7.0$, d.f. = 1, $p = 0.008$ using all usurpers). Employing these data in a simple algebraic calculation yields an estimate of 12.6 per cent for the overall rate of ISI as chicks in territory acquisitions (see the electronic supplementary material, Box S1). NHPI therefore appears to impact habitat selection at least as strongly as ISI as chicks (see figure 3).

(d) Does natal habitat preference induction wane on second territories?

Although the occurrence of NHPI shows that loons retain the capacity to identify natal-like lake characteristics from the chick stage to first settlement at ages 4–11, NHPI appears to weaken when loons settle on second breeding lakes. Among a subsample of the original 102 loons that settled first on one territory and then another ($n = 22$), NHPI was evident on first settlement lakes (empirical ED = 1.14, expected ED = 1.60, two-tailed $p = 0.010$), as in the overall sample, but natal and second settlement lakes did not differ significantly from expected (empirical ED = 1.50, expected ED = 1.58, $p = 0.610$). Yet ED between natal and first settlement lakes did not differ significantly from that between natal and second settlement lakes (mean difference = 0.133, paired $t = 0.478$, d.f. = 21, $p = 0.637$), so this result is tentative.

4. Discussion

(a) Natal habitat preference induction or a silver spoon effect?

Loons might have settled on breeding lakes similar to their natal ones not because of NHPI, but because of a 'silver spoon effect', whereby animals reared on favourable natal habitats develop into strong competitors as adults [36]. The effect is plausible in loons, because large, high-pH lakes produce more young, which survive at a higher rate than those from small, acidic lakes [27]. If competition is vigorous for large, alkaline lakes, and loons reared on such lakes are stronger competitors for them, then loons reared on small, acidic lakes might be forced to breed on small, acidic lakes. However, three lines of evidence argue against the silver spoon effect. First, a variety of territories are always available. In 2012, 20 of 118 territories in the main study area that had produced nests or chicks since 2005 were vacant, including seven lakes of larger than median size and six lakes of larger than median pH. Second, over one-third of all territories are acquired by founding in vacant lakes, which entails little or no interaction with conspecifics, and which is impacted strongly by NHPI. Third, large, alkaline lakes do not produce strong competitors. Natal lakes from which usurpers come (mean size: 64.4 ha \pm 59.2 s.d., $n = 24$) are not significantly larger than natal lakes of founders (81.5 ha \pm 58.1 s.d., $n = 32$; $t = 1.08$, $p = 0.284$, d.f. = 54) and are, in fact, slightly more acidic (pH = 6.74 \pm 0.75 s.d., $n = 24$) than natal lakes of founders (pH = 7.17 \pm 0.73 s.d., $n = 32$; $t = 2.16$, $p = 0.035$, d.f. = 54).

(b) Natal habitat preference induction or an inherited preference?

Although NHPI is generally thought to occur because an animal learns cues from the natal habitat that it later uses to settle in a breeding space [20], settlement in natal-like habitat by young prebreeders could also reflect a heritable habitat preference [25,37]. The apparent diminishment of NHPI on second territories suggests that the phenomenon can be influenced by experience, supporting the view that the pattern is learned and not inherited. However, cross-fostering of loon chicks will be required to determine decisively whether NHPI has an environmental or genetic origin.

(c) Natal habitat preference induction versus other means of habitat selection

This first-ever comparison of NHPI with ISI in a natural population reveals that habitat settlement involves diverse strategies, and is influenced by both private information (i.e. that possessed by a single animal and not shared [8]) and public information (that shared by multiple animals [8]). Our findings suggest that NHPI is of similar or greater importance to habitat selection compared with the use of ISI as chicks, a settlement strategy by which loons acquire productive territories [28].

If NHPI is used chiefly by young non-breeders searching for a first territory, as our preliminary data suggest, an animal's approach to habitat selection might exhibit a temporal dynamism that is currently underappreciated. Apparently, a young prebreeder that returns to the breeding ground and finds a natal-like lake that is vacant tries to found a territory there. If occupied, the young loon often attempts to usurp the territory [32] after a lag of a few years (W. H. Piper 2013, unpublished data). Natal-like territories that produced chicks the previous year are doubly attractive to prebreeders. Once displaced from its first territory, loons appear to use NHPI less or not at all in selection of a second territory.

(d) Natal habitat preference induction in both sexes

Male loons achieve greater useful familiarity with their territories than do females, as they control the placement of nests and enjoy higher reproductive fitness over time as a consequence [38]. Yet the sex bias in site familiarity does not seem to reflect a general tendency of males to cue on attributes of their aquatic habitat, as the nesting pattern is not echoed in NHPI, which is strong in both sexes. This fact suggests that NHPI is of more fundamental importance to individual fitness, perhaps conferring a survival benefit to all individuals. We have insufficient data, at present, to examine the fitness impact of the behavior.

(e) Proximate and ultimate causes of natal habitat preference induction

It is unclear how loons detect environmental attributes, lake size and pH, on which NHPI is based. While the relative size of a potential breeding lake to its natal one might be determined by quick visual inspection, acidity seems more difficult to assess, owing to a shortage of taste receptors and insensitivity to acidity in birds [39]. Perhaps loons detect not pH *per se*, but a correlate such as diversity of piscine and/or invertebrate prey [40].

Most studies of habitat selection focus on its potential to promote reproduction, not survival [13], but NHPI seems likely to promote the latter. In fact, young animals chiefly learn skills like foraging and predator avoidance in their first few weeks and months of life [41], and probably little or nothing about the quality of breeding habitat and the presence of safe nesting or birthing zones. Thus, cues learned from the natal habitat would seem more likely to increase survival than reproductive success. The puzzling settlement of loons on lakes that match their natal lake in size and pH, instead of large, high-pH lakes, which produce more and fitter young [27], further supports the view that survival, not reproductive success, might be a fitness benefit of NHPI. If so, we

might predict that NHPI would tend to occur more often in long-lived species such as loons, which may breed for a decade or longer, than in species that live and breed for only a few years.

NHPI might promote survival if skills learned as a juvenile become foraging specializations [20] that help an animal maintain body condition throughout life. Moreover, a link between natal-like habitat and condition could explain the proximate basis of NHPI. For example, a young loon might settle on a natal-like lake because of the energetic advantages of so doing and breed there merely because a potential mate does likewise. Thus, NHPI could be a by-product of a young animal's effort to maintain good body condition.

(f) Why is natal habitat preference induction reported so rarely?

A baffling fact about NHPI is that it is reported rarely, despite the expectation of many workers that it should be common [13]. To be sure, the nature of loon habitat and natal dispersal provided us a good opportunity to detect NHPI. Most loon territories are whole lakes with unambiguous borders, whose physical, chemical and biotic features have been measured and found to vary greatly from one lake to another. In contrast, the breeding spaces of most terrestrial animals contain a rich assortment of vegetation types and environmental features that defy or complicate quantification [42–44]. In addition, territory boundaries of many animals fluctuate over time [45], and must often be mapped laboriously through repeated observations [46] or simulated intrusions [47].

While the loon system gave us a window onto NHPI that most workers lack, NHPI is likely to occur widely in animals. Its occurrence is well known from captive studies, especially in insects (reviewed by Davis & Stamps [20]). Recent field investigations, though indirect [48–50] or problematic [26,34,51], suggest that NHPI might be widespread [13,52].

In conclusion, our findings and those of numerous captive investigations suggest a greater role for NHPI in habitat selection than currently realized. We must hope that other investigators tackle the dual problems of tracking natal dispersal and quantifying habitat attributes so that we can gain an understanding of the frequency of NHPI in animals generally. Only then will we be able to determine whether this phenomenon helps explain the failure of many species to settle in breeding habitat of highest apparent quality [5,14].

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Data accessibility. Data from this paper are accessible to the public through eCommons@cornell.edu via <http://hdl.handle.net/1813/13098>, following a two-year delay.

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