

Nestsite selection by male loons leads to sex-biased site familiarity

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Summary

1. The concept that animals benefit from gaining familiarity with physical spaces is widespread among ecologists and constitutes a theoretical pillar in studies of territory defence, philopatry and habitat selection. Yet proximate causes and fitness benefits of site familiarity are poorly known.
2. We used data from marked common loons *Gavia immer* breeding on 98 territories over 14 years to investigate the ‘win–stay, lose–switch rule’ for nestsite placement (if eggs hatch, reuse nestsite; if predator takes eggs, move nestsite). Males controlled nest placement in this species: pairs used the rule if both members remained the same from the previous nesting attempt or if only the male remained the same but not if only the female remained the same.
3. By means of the nesting rule, male common loons benefited from site familiarity, increasing nesting success by 41% between their first and third years on a territory. In contrast, females exhibited no increase in nesting success with increased territorial tenure.
4. Owing to site familiarity, a male loon competing for a breeding territory faces a considerable ‘familiarity deficit’ compared with the male breeder already established there. The familiarity deficit probably explains why resident animals often fight hard to retain familiar territories, when challenged, and why animals of many species tend to remain on familiar territories rather than moving when territories of higher intrinsic quality become available nearby.

Key-words: dispersal, habitat selection, resource value, site-fidelity, territoriality.

Introduction

A widespread and enduring belief among behavioural ecologists is that animals benefit from familiarity with physical spaces (Tinbergen 1953; Hinde 1956; Waser & Wiley 1980; Greenwood & Harvey 1982; Stamps 1995; Harwood *et al.* 2003). This presumption has important ramifications for diverse topics within behavioural ecology, including philopatry, aggression, habitat selection, migration and population dynamics. In addition, the concept of adaptive site familiarity constitutes a cornerstone of numerous behavioural models (e.g. Maynard Smith & Parker 1976; Enquist & Leimar 1987; Switzer 1993; Stamps 1995; Matthiopoulos, Harwood & Thomas 2005). In light of its far-reaching impact for students of behaviour, it is curious that empirical evidence for adaptive site familiarity is fragmentary and largely indirect (Stamps 1995).

Two conspicuous behavioural patterns suggest that site familiarity might be valuable. First, most animals consistently dominate opponents in aggressive interactions within familiar areas (the ‘resident advantage’; reviewed by Kokko, Lopez-Sepulcre & Morrell 2006), even in cases where contestants do not differ in body size (Hack, Thompson & Fernandes 1997; Johnsson & Forser 2002). Second, many animals travel hundreds or thousands of kilometres and face myriad hazards to return to precise locations that they had used in a previous season (e.g. Gratto, Morrison & Cooke 1985; Limpus *et al.* 1992). Consistent return to an exact location implies that the association with a familiar space provides a compensating benefit (Stamps 1995). Yet the resident advantage and spectacular feats of homing only call attention to the question of what proximate factors make familiar space so valuable.

We have a rudimentary understanding of proximate factors that might contribute to site familiarity. Spatial memory is undoubtedly important. A diverse array of animals can learn and recall locations of food, landmarks and other features of familiar areas in laboratory or seminatural surroundings (electric fish *Gnathonemus petersii*: Cain, Gerin & Moller

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1994; crows and jays, family Corvidae: Balda & Kamil 1998; honeybees *Apis mellifera*: Dyer 1996; turtles, *Pseudemys scripta*: Lopez *et al.* 2000; ants, *Lasius niger*: Devigne & Detrain 2006; ground squirrels, *Spermophilus columbianus*: Vlasak 2006) and in nature (ovenbirds *Seiurus aurocapillus*: Zach & Falls 1979). Furthermore, captive animals have shown the ability to become familiar with enclosures so as to elude predators more efficiently over time (Metzgar 1967; Brown 2001). Stamps (1995) suggested a novel mechanism, proposing that animals might come to use serial motor patterns efficiently over time within familiar space as a means to avoid obstacles.

While we have only begun to understand proximate mechanisms that might lead to site familiarity, its fitness impact is even less well known. Indeed, our surprising lack of knowledge concerning fitness consequences of site familiarity has made plausible the hypothesis that it confers no benefit. For example, Davies (1978) and Yasukawa & Bick (1983) have argued that the chief importance of site familiarity might be as a conventional rule ('resident wins, intruder loses') to settle territorial contests at low cost. The willingness of ecologists to suppose that site familiarity might have no advantage underscores our tentative understanding of this topic.

A promising behaviour pattern that might be exploited to investigate proximate causes and fitness consequences of site familiarity is the 'win-stay, lose-switch' rule (hereafter 'the WSL rule') used by breeding animals (Switzer 1993; Haas 1998; Hoover 2003). The WSL rule involves selecting a site for breeding based on the success or failure of the previous breeding attempt. An animal employing the rule simply reuses a site if the previous breeding attempt at that site produced young, but moves to a new location if that attempt failed. Scores of animals, especially birds, use the WSL rule (e.g. Richdale 1957; Catchpole 1972; Newton 1976; Blancher & Robertson 1985; Lindberg & Sedinger 1997; Olsson, Gullberg & Tegelstrom 1997; Switzer 1997; Haas 1998; Kokko, Harris & Wanless 2004; Styrsky 2005). As a simple, well-defined behaviour pattern that links recent experience in a space with a likely increase in fitness there, the WSL rule could be viewed as the smallest potential 'unit' of adaptive site familiarity.

Two recent studies suggest that the WSL rule does, in fact, result in fitness gain and thus could serve as a foundation for adaptive site familiarity. Wood ducks *Aix sponsa* and prothonotary warblers *Protonotaria citrea* both used the WSL rule (Hepp & Kenamer 1992; Hoover 2003), and reproductive success improved in both species by this means. Unfortunately, the exclusive use of artificial nestboxes in both studies makes them imperfect exemplars of adaptive site familiarity.

We examined nestsite selection in the common loon *Gavia immer* to look for evidence of adaptive site familiarity. Loons would appear likely to benefit from site familiarity because: (1) the species is long-lived; (2) individuals tend to use the same small breeding lake for many consecutive years; and (3) lakes are consistent in shape, size and topography between years. Placement of nestsites offered a promising avenue for study in this species, as nests occur in plain view (in contrast to those of most animals; see Jehle *et al.* 2004) and chiefly at natural sites. Most importantly, loons use the

WSL rule in selecting nestsites (Strong, Bissonette & Fair 1987; McIntyre 1988).

Materials and methods

STUDY AREA AND SPECIES

Our investigation took place within an oval-shaped study area (60 km along north-south axis \times 30 km along east-west axis) that covered central Oneida County and portions of southern Vilas and northern Lincoln County, Wisconsin (centre of study area at 45°41'N, 89°36'W; see also Piper *et al.* 1997a). This region contains 386 lakes large enough to be used by loons (\geq 4 ha), of which most are shallow (\leq 20 m maximum depth), seepage lakes and 42% contain islands. All lakes are bordered by a combination of upland forest (second growth, mixed deciduous and coniferous), marsh and sphagnum bog. Human development occurs along at least 60% of the perimeters of most lakes, although development varies from 0 to 100% within the study area. Nesting areas used by loons included islands (37% of all nests described, $n = 846$), emergent mounds of soil and vegetation (15% of nests) and shorelines (48% of nests).

The common loon is a large diving bird that breeds in lakes in northern North America and winters in coastal oceans of the continent. Loons are sexually dimorphic (mean \pm SD; males: 4508 \pm 299, $n = 219$; females: 3619 \pm 221, $n = 205$). Pair members defend all-purpose territories beginning in April, when ice-out occurs, and nest in May and June. Nests are built by both male and female and usually occur on mounds consisting of several kilograms of aquatic vegetation. They are placed within 2 m of the water's edge, often on marshy hummocks or islands, and pairs jointly incubate two-egg clutches. Only 48% of all nests ($n = 941$) hatch chicks, the chief cause of nest failure being egg predation by raccoons *Procyon lotor* (roughly 80% of all egg predation in Minnesota, McIntyre 1988; 83% of all identified predators in northern Wisconsin, McCann, Haskell & Meyer 2005). Egg predation is easy to ascertain, in most cases, as eggshell fragments can be found within 5 m of the nest. Abandonment is a second cause of nest failure (12% of all nest attempts) and can result from eviction of a pair member, flooding or blackfly infestation (Piper *et al.* unpublished). Following nest failure, pairs renege up to three times within a season. If incubation proceeds for the entire 28-day incubation period, pairs rear the chick or chicks to independence, at 11 weeks of age (McIntyre & Barr 1997). All chicks reared by a mated pair are their genetic offspring, as no extrapair copulations or fertilizations occur (Piper *et al.* 1997b).

Length of tenure on a territory averages several years in both males (mean duration of tenure \pm SD, 5.7 \pm 4.4 years, $n = 33$) and females (4.6 \pm 3.8 years, $n = 19$). However, changes in pair membership do occur, chiefly through territorial take-over (51% of all territory acquisitions in males; $n = 127$; 47% in females; $n = 115$). Territorial take-over, or 'eviction', follows a consistent formula in each sex: a male or female displaces the pair member of its own sex and then pairs quickly with the remaining resident (Piper, Tischler & Klich 2000). Two less common modes of territory acquisition are founding of new territories in vacant areas (28% and 30% of male and female acquisitions, respectively) and passive replacement of dead residents (21% and 23%).

The study area consisted of 12 loon territories in 1993, but this number gradually increased until 2006, when 95 territories were covered. Territories were of three kinds: (1) partial lake, which comprised part of a large lake ($>$ 100 ha); (2) whole lake, made up of one entire lake (usually 20 ha or greater); and (3) multilake, consisting of two or more small lakes (4–20 ha; see Piper *et al.* 1997a).

CAPTURE AND OBSERVATION OF LOONS

Adult loons and chicks were netted at night by spotlighting from a small motorboat and fitted with a unique combination of coloured leg bands and a USFWS metal band. Throughout the nesting season (May–July), observers made hour-long visits to each focal territory one to three times weekly during which both pair members were identified by leg bands, and territorial behaviour and nesting attempts were monitored. On limited occasions, tameness of the pair and weather conditions permitted detailed observation of nesting behaviour, including recording of specific roles of each sex.

NESTSITE-MAPPING AND STATISTICAL ANALYSIS

Nest locations were plotted on maps (from 1993 to 2000) or with handheld GPS devices (2001–06) and inter-nest distances computed with GIS software (ArcView 3.2a; ESRI, Inc., Redlands, CA, USA). As our goal was to determine predictors of nestsite movements, the outcome variable was 'distance from site used for last attempt'. Six potential predictors were tested: year (1993–2006), territory (among 98), absolute change in water level from last attempt ('water level'), whether or not female had changed since the last attempt ('female turnover'), whether or not male had changed ('male turnover'), and success (i.e. hatching) or failure (i.e. predation) of the previous nest ('previous success'). We treated all consecutive nesting attempts the same in our analysis, whether they occurred within or between years. Abandonments were excluded from the analysis because of their relative scarcity, as were cases in which loons nested on artificial platforms (see Piper *et al.* 2002). The records consisted of many consecutive nesting attempts within territories; hence, a repeated measures design was used that employed territory as the grouping variable ('xtreg' command in STATA 8 software program, College Station, TX, USA). Models were developed by including only predictors for which $P < 0.25$ in the univariate model, placing all qualifying predictors into a multivariate model, adding all first-order interaction terms, and eliminating all terms that did not reach significance ($P < 0.05$) from least to most significant.

Following the finding that the sex of pair members affected nest placement, a second analysis was used to learn if sex of pair member affected nesting success, which could take on values of 'hatched' or 'suffered predation', and hence was binary. Predictors tested were number of years that male had nested on the territory, years that female had nested on the territory and another variable found to affect loon nesting success: absolute change in water level. Again, we used a repeated measures analysis ('xtlogit' command in STATA), employed territory as the grouping variable, excluded data from abandoned nests and proceeded as above with model selection.

Results

NESTSITE SELECTION AT NATURAL SITES AND ITS FITNESS CONSEQUENCES

Behavioural observations on pairs during the pre-nesting period seemed to indicate a strong role for males in nestsite selection. In 23 of 26 pairs monitored closely, the male exhibited more nest-searching or nest-building (binomial test, $P = 0.000088$, two-sided).

In the analysis of the predictors of nestsite movement, only lake size, previous success, male turnover, and the interaction of previous success \times male turnover reached statistical significance

Table 1. Predictors in the final repeated measures model that used 'distance from site used for last attempt' as the dependent variable and 'territory' as the grouping variable. Wald $\chi^2_4 = 24.23$, $P < 0.0005$ for the overall model. Though nonsignificant in the presence of the previous success and previous success \times male turnover terms, male turnover was left in the model (Table 1) to ensure stability of coefficients (Braumoeller 2004)

Predictor	<i>z</i>	<i>P</i>
Previous success	-4.05	0.000
Male turnover	-1.47	0.142
Previous success \times male turnover	3.02	0.003
Lake size	1.98	0.047

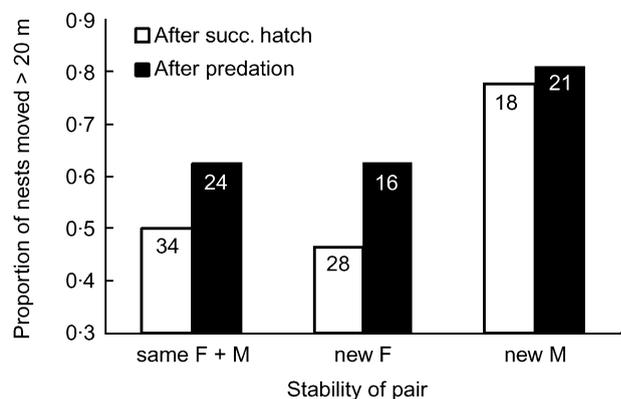


Fig. 1. The impact of male turnover within a nesting pair on the distance moved from previous site. Pairs in which both members were the same as for the last nesting attempt and pairs with the same male and a new female tended to use the 'win-stay, lose-switch' rule. Breeding pairs with the same female and a different male, however, almost always nested far from the previous location and did so without regard to nesting success. Numbers at the tops of bars indicate sample sizes; within each pair type, no individual loon appears more than once.

at any stage. All remained in the final model (Table 1). While the marginal significance of lake size indicated merely that nests tended to move farther on large lakes, and the significance of previous success confirmed use of the WLS rule, the substantial significance of the previous success \times male turnover interaction showed that a pair's use of the rule depended upon whether the male was the same as for the last attempt. When the male was the same (whether or not the female changed), pairs used the WLS rule, tending to reuse nestsites after hatching chicks and move after failure (Fig. 1). When the male had changed, pairs moved farther between nestsites, and this did not depend on previous success or failure.

The tendency for reproductive success to increase with tenure in breeding spaces is common in animals and has a number of possible explanations. First, age or improvement in the performance of essential breeding behaviours over time might cause the pattern (Thomas & Coulson 1988; Bregnballe 2006). If so, males that moved from a first territory where they had bred successfully to a new, unfamiliar territory (usually because of eviction) should have achieved reproductive

success that reflected their age or breeding experience. In fact, only six of 17 male loons with breeding experience (35%) hatched chicks in their first year after moving to a new lake, which is far below the mean rate of annual chick production among males with comparable experience on familiar territories (70.5%; $n = 322$ male-years; binomial test: $P = 0.003$). Second, males that often shifted between territories and had poor reproductive success could have produced a downward bias in hatching success among first-year males. However, most new males within the sample were, in fact, individuals that had bred successfully elsewhere and/or remained for several years on territory.

SELECTION OF ARTIFICIAL NESTING PLATFORMS AS NESTING SITES

Artificial nesting platforms were attractive nest sites for males new to a territory. While only seven of 34 new males nested within 20 m of the nest site of the previous male in territories lacking platforms, five of seven new males in territories with platforms placed their initial nest on the same platform used by the previous male (Fisher's exact test: $P = 0.016$). Furthermore, males in their first year of residency on a territory hatched chicks in 11 of 14 (79%) attempts, as compared with 39 of 101 at natural sites (39%; Fisher's exact test: $P = 0.008$). Thus, new males tended to use nesting platforms as nesting sites and enjoyed immediate fitness benefits from so doing.

Discussion

EVOLUTION OF THE WSLS RULE

The WSLS rule appears to have evolved in response to nest predation inflicted on loons by raccoons. Males that must place the nest along a shoreline in the absence of islands or floating hummocks (47% of all nests, $n = 952$) cannot accurately assess the safety of nest sites, because raccoons forage nocturnally. Lacking information on space-use patterns of local raccoons, male loons appear to locate nests by trial and error. Moreover, nest sites that fail or succeed in one attempt tend to experience the same result on the next attempt (see Switzer 1993), because of consistent home range use of raccoons between years (see Lotze 1979). Hence, the WSLS rule works. Finally, raccoons often live for only 2–3 years (MacClintock 1981), and territory tenure of a male loon is likely to be much longer (Piper *et al.* 2000). Thus, individual predators die and new ones colonize the area used by a nesting pair. The rule accommodates this dynamic, as it allows for rapid shifts in location following predation.

The widespread use of the WSLS rule by vertebrates, especially birds, indicates that predation pressure faced by loons during reproduction is similar to that faced by many other species. Evidently there is enough constancy in patrolling patterns of individual nest predators (chiefly mammals) or such limited capacity of animals to identify safe nest sites by mere inspection that many species must resort to trial and error.

The WSLS rule, which concerns only consecutive nest sites, is probably just a special case of a more sophisticated,

longer-term strategy (Schjorring, Gregersen & Bregnballe 2000). Animals that breed in the same space over several years most likely accumulate a spatiotemporal memory of all breeding sites they have used. Thus, they probably select a breeding site by integrating information at known sites, including success rate, recency of use, and continued suitability of the site. Further collection of longitudinal nesting data will test the hypothesis that the WSLS rule is part of a longer-term strategy that might be termed 'win–return, lose–avoid'.

THE ESSENCE OF FAMILIARITY

Many workers cite familiarity with neighbours (e.g. the 'dear enemy' phenomenon; Temeles 1994) and mates as an important means by which animals benefit from site-fidelity, and a large literature supports this assertion (e.g. Beletsky & Orians 1989; Stamps 1991; Eason & Hannon 1994; Schjorring *et al.* 2000). However, knowledge of permanent physical (e.g. topography) and biotic (e.g. vegetational) features of a space is likely to be a widespread advantage of site familiarity because such features characterize any inhabited space, while social environment varies depending upon social structure, habitat distribution and population density. Systematic comparison of both 'social familiarity' and 'spatial familiarity' will be required to learn the relative importance of each.

NEST SITE SELECTION BY MALES

While a huge literature deals with the habitats and microhabitats birds select for nesting (e.g. Martin & Roper 1988; Martin 1998; Warkentin *et al.* 2004; Davis 2005), our understanding of the process by which mated pairs choose nest sites, especially the relative importance of males and females in the process, is minimal. Stamps *et al.* (2002) have concluded that nest site selection in birds is often a 'joint decision' between members of mated pairs, while Graber, Davis & Leslie (2006) have suggested that nest site selection by songbirds, long considered the role of the female, might involve a substantial male contribution. These assertions, however, rest solely on behavioural observations and lack an objective determination of each pair member's role in nest site selection.

The restriction of nest site placement to male loons is difficult to explain from a strict adaptationist perspective. One might have expected a system whereby a pair member new to a lake would defer to a mate with experience nesting there, because both sexes stand to benefit from having an individual select the nesting site that has knowledge of nesting histories at past locations. However, males that take ownership of a territory do not benefit from their mate's nesting experience; instead, they 'start from scratch', learning for themselves where to nest by trial and error. Thus, male-only nest site selection has steep fitness costs for both sexes. None the less, we can offer a few hypotheses for this pattern. First, having one pair member always choose the nest site is simple and minimizes the possibility of behavioural conflict between pair members, which could delay the nesting effort. This hypothesis, however, fails to predict which sex should choose. Second, male control of

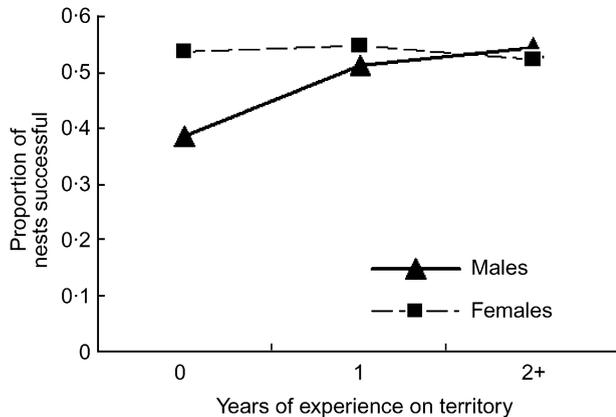


Fig. 2. Hatching success of males and females as a function of territorial tenure, ignoring their mates' experience. Males experienced an improvement in hatching success during their territorial tenure, while females did not.

nest-site placement might have evolved if males, which are much larger than females, position nests so as to facilitate defence of them and then act as the chief defenders of the nest (J. Stamps, pers. comm.). A preliminary examination, though, indicates that male and female loons do not differ in the extent of their nest defence (Piper unpublished). A third explanation, unappealing because it is not testable without an onerous comparative approach, is that nest placement in common loons reflects their phylogeny, and its ultimate cause therefore is shrouded in the evolutionary past.

If sex-biased familiarity with breeding sites occurs in other animals, it might prove to be a key ecological cause of sexual differences in site-fidelity and territory defence. In common loons, for example, male-biased site familiarity increases 'resource value' in this sex (see Leimar & Enquist 1984) and seems a likely cause of vigorous acoustic territorial defence by males that often culminates in the death of territorial residents in battle (Piper *et al.* in press).

IMPACT OF SITE FAMILIARITY ON HABITAT SELECTION: THE FAMILIARITY DEFICIT

In species that gain familiarity with breeding patches over time, new residents unfamiliar with a patch face a period of reduced reproductive success there because of their lack of familiarity (see Fig. 2). The reduction in fitness of a new resident in a patch compared with a long-term resident that has accumulated knowledge of nesting sites can be termed the 'familiarity deficit'.

The classical models for habitat selection (Fretwell & Lucas 1969; Fretwell 1972) assume clear differences in intrinsic quality between breeding patches and no familiarity deficit. A large familiarity deficit diminishes the importance of any differences in intrinsic quality between breeding patches. Even if patches differ substantially in intrinsic quality, an owner that has overcome the familiarity deficit through years of residency within a territory will likely achieve higher reproductive success there than at another patch of higher

intrinsic quality. Indeed, the familiarity deficit is a likely explanation for the reluctance of many territory holders to move to vacant breeding habitat of high quality when it becomes available (Krebs 1971; Searcy 1979; Lanyon & Thompson 1986; Aebischer & Coulson 1990).

The familiarity deficit is not fixed for a population, but varies between territories according to the habitat they contain. In territories containing obvious, high-quality nesting habitat (in loons, such habitat consists of small islands far from shore), the familiarity deficit is small; hence, resource value for residents differs little from that for intruders that might evict them. As a result, intruders should be aggressive and evictions frequent in such territories. Conversely, territories containing no obvious nesting habitat exhibit a large familiarity deficit and should see few evictions.

Acknowledgements

We thank Harold Dyck and Rita Petersen of the UCI Center for Statistical Consulting for guidance concerning statistical tests. We also thank Kate Lessells, Hanna Kokko, Ken Norris and an anonymous reviewer for comments on the manuscript. The following research assistants contributed to this study: Keren Tischler, Margaret Perala, Nathan Banfield, Marc Schwabenlander, Amy Turcotte, Erin Harrington, Eric Witham, Tim Larsen, Eric Coonradt, Julie Mao, Len Liu, Curt Jacoby, Michele Parara, Michael Nelson, Peter Keith, Curan Bonham, Kristen Potter, Ainsley Seago, David Latremouille, Michelle Gojkovich, Brad Lampe, Duncan Reid, Matthew Gibbons, Rachel Hart, Alyson Webber, Carly Michie, Mandi Reiman, Jason Reiman, Elizabeth Summers, Jesse Schwingle, Max Bockes, Ehren Banfield, Erin Snell, Kristin Pufpaff, Jessica Ciske and Lauryn Linsell. We thank many landowners who provided access to their lakes. Funding was provided by the National Science Foundation, National Geographic Society, Environmental Protection Agency, Disney Conservation Fund, Sigurd Olson Environmental Institute, North American Loon Fund, Chapman University and Cornell University.

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Received 2 March 2007; accepted 21 September 2007

Handling Editor: Kate Lessells