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RESEARCH PAPER
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Influence of pool habitat characteristics on Red-throated Loon *Gavia stellata* occupancy and reproduction in a Boreal forest landscape

Smålommens Gavia stellata *uppträdande och reproduktion i relation till habitategenskaper i häckningstjärnar i ett borealt skogslandskap*

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WE INVESTIGATED the occupancy of alternative breeding pools for Red-throated Loon *Gavia stellata* and the reproductive output in relation to a selection of habitat characteristics in a coniferous forest inland area in south-central Sweden, using generalized linear mixed models. Models provided good support for the conclusion that small-sized pools with high coverage of floating vegetation were preferred. The survival of pre-fledged chicks was higher when foraging waters were located closer, and open mires around the breeding pool were more extensive. We propose that these habitat characteristics should be considered in nature conservation planning and management, as well as in environmental impact assessments. We found that with the current data, predicting pool occupancy and chick survival based on the selected habitat characteristics was not sufficiently

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accurate to replace field surveys and can only be used as a complementary method. We also emphasize the importance of freshwaters, potentially to be used for foraging in the surrounding landscape, which is an often-overlooked aspect in management and impact assessments.

Keywords: waterbirds | fish-eating birds | breeding success | population management | environmental impact assessments

Introduction

The Red-throated Loon *Gavia stellata* is an overall rare breeding bird species in Sweden, with a population of 1,300–1,900 pairs (Ottosson *et al.* 2012). Like all loon/diver species (Gaviidae), it is a fish-eating bird species and it has a circumpolar distribution in the taiga and tundra landscape of the Northern Hemisphere. In contrast to the four other loon species, the Red-throated Loon primarily breeds at small water-bodies, often smaller than 1 ha (Gomersall 1986, Okill & Wanless 1990), and which we refer to as pools in this study.

Mostly, the breeding pools are devoid of fish, and the chicks are fed by prey from larger freshwater lakes or at sea up to 8–9 km from the breeding sites, rarely further away (Merrie 1978, Douglas & Reimchen 1988, Eberl & Picman 1993, Eriksson & Johansson 1997). Thus, the management of a Red-throated Loon population has to consider a landscape perspective, taking into account the breeding sites as well as the foraging waters, and the flight routes between them. Identification of potential breeding sites is important for the successful conservation of the species, and a better understanding of the influence of habitat characteristics on pool occupancy and reproduction could therefore contribute to improved management.

There is a long-term dynamic in the selection of breeding pools. Breeding sites may be abandoned, reoccupied, or newly established over a timescale of several years or even decades (Eriksson & Åhlund 2013), and nest predation seems to be one of the driving forces (Dahlén & Eriksson 2002).

The Red-throated Loon has been a matter of concern in bird conservation for a long time. Globally, it is classified by the IUCN as 'Least Concern' but declining (BirdLife International 2022). The species is listed in Annex 1 of the EU Birds Directive, which means that 'it shall be the subject of special conservation measures concerning their habitat in order to ensure their survival and reproduction in their area of distribution' (Article 4.1 of the Directive, European Parliament 2009). In the EU, the long-term trend of the breeding population is increasing, while the short-term trend for the period 2013–2018 is stable, as indicated by the assessment of bird species' status and trends in line with Article 12 of the EU Birds Directive (https://nature-art12.eionet.europa.eu/article12/summary?period=3&subject=Gavia+stellata&reported_name=).

In Sweden, there are indications of a long-term declining trend (Svensson *et al.* 1999). Several small lakes and pools known as 'Lomtjärn' (English: 'Loon Tarn') and similar but without recent breeding records indicate that the species might have been more common and wide-spread historically. More recent surveys under the umbrella of The Swedish Bird Survey (Svensk Fågeltaxering, https://www.fageltaxering.lu.se) indicate an increasing trend in the adult population for north and central Sweden (Green *et al.* 2022), although a long-term declining trend in the breeding success (Eriksson 2019) raises concern. Potential reasons for these seemingly contradictory trends are briefly discussed by Eriksson (2019).

For Red-throated Loons breeding in an inland forest landscape and depending on freshwaters for foraging, previous studies of relationships between habitat characteristics and the breeding success have been based on univariate regressions (Eriksson *et al.* 1988, Eriksson & Johansson 1997, Dahlén & Eriksson 2002). These studies included *inter alia* surface area of pools, distance to closest freshwater lake used for foraging, distance to road (as an indicator of accessibility and potential disturbance from human activities) and occurrence of appropriate breeding islets. Only one relationship was found: the number of fledged chicks per breeding pair was negatively associated with the distance between the breeding site and foraging lake, within a range of 0.7–13.1 km, in one of the studies (Eriksson & Johansson 1997).

For a Red-throated Loon population breeding in the coastal region of Västerbotten, northern Sweden, and foraging at sea, Skyllberg *et al.* (1999) found that breeding success was higher at pools characterised by a mosaic of open water, high-grown sedge (*Carex* spp.) and *Sphagnum* moss mats. No association was found with the surface area of pools or distance to sea, within a range of 0.3–4.0 km.

More recently, Lehtonen (2016) and Olsson *et al.* (2021) investigated potential environmental variables that might be associated with the presence of breeding Red-throated Loon and with their breeding success at Holmöarna Archipelago in the Gulf of Bothnia. Also, here the Red-throated Loon catches fish prey in the surrounding sea. However, the result of the two studies were not consistent, although the same Red-throated Loon population was targeted. Lehtonen (2016) concluded, on the basis of data over four years, that breeding success increased with a high lake area/perimeter ratio and with a shorter distance between breeding pool and the sea, within a range of 0.2–1.5 km. Olsson *et al.* (2021) recorded that occupancy of breeding pairs in 43 alternative pools during a period of seven years was positively related to vegetation cover and the distance to the sea, within a range of 0.2–3.0 km, while the breeding success was negatively but not significantly related to pool surface area and distance to sea (Table 3 in Olsson *et al.* 2021).

The identification of breeding sites is of main concern in environmental impact assessments (EIAs) for various projects where populations of Red-throated Loon might be affected, given the rarity of the species, its reduced breeding success, and its listing on Annex 1 of the EU Birds Directive. The long-term dynamics of breeding pool occupancy make it also necessary to consider temporarily abandoned pools in EIAs, which is why field surveys done during only one or a few breeding seasons rarely provide enough information for appropriate assessments. Thus, the question has been raised asking if mapping of habitat characteristics of pools is a possible alternative, in order to reliably identify whether a pool is a potential Red-throated Loon breeding pool, or not. This would result in a considerable increase in survey efficiency since such habitat characteristics can usually be recorded during a single visit. Therefore, the aim of this study was to investigate whether the use of potential breeding pools, the breeding success and the survival of non-ledged chicks of Red-throated Loon is linked to various habitat characteristics, and if so, how accurately occupancy and breeding success can be predicted based on those habitat characteristics.

STUDY AREA

The study area was located in Malung-Sälen Municipality (60°41'N, 13°43'E) in the County of Dalarna, south-central Sweden (Figure 1), in the core area of the Swedish population of Red-throated Loon. Dalarna together with the neighbouring counties (Värmland, Örebro and Västmanland) harbour a total of 470–600 pairs, or about one third of the total population in Sweden (concluded from Ottosson *et al.* 2012). Fish for the chicks are almost exclusively caught in nutrient-poor freshwater lakes with a good supply of small-sized cyprinid or salmonid fish (Eriksson 2006, Eriksson & Paltto 2010).

The size of the study area was approximately 1,820 km^2, and the same area was covered by Dahlén & Eriksson (2002) in a previous study of the breeding biology of the target species during 1991–2000. The area hosts a population of around 70 Red-throated Loon pairs that have been surveyed on an annual basis since the 1990s. The presence of a territory-holding or stationary pair has been recorded in at least one year in 101 pools, which reflects some dynamics in the occupation of alternative breeding sites. 15–20 nutrient-poor clear-water lakes are used for foraging, with distances ranging from less than 0.1–4.9 km between breeding pools and foraging lakes. For this study, results from the field surveys during the period 1994–2019 have been used.

Having in mind that nest predation has been identified as a main reason for breeding failures in previous studies of Red-throated Loon in our study area (Dahlén & Eriksson 2002) as well as elsewhere (Eberl & Picman 1993, Skyllberg *et al.* 1999, Hulka 2010, Rizzolo *et al.* 2014, Olsson *et al.* 2021), it is relevant to inform that *inter alia* Red Fox *Vulpes vulpes*, American Mink *Mustela vison*, Common Raven *Corvus corax*, Common Crane *Grus grus* and more occasionally Western Marsh Harrier *Circus aeruginosus* have been identified as nest predators.

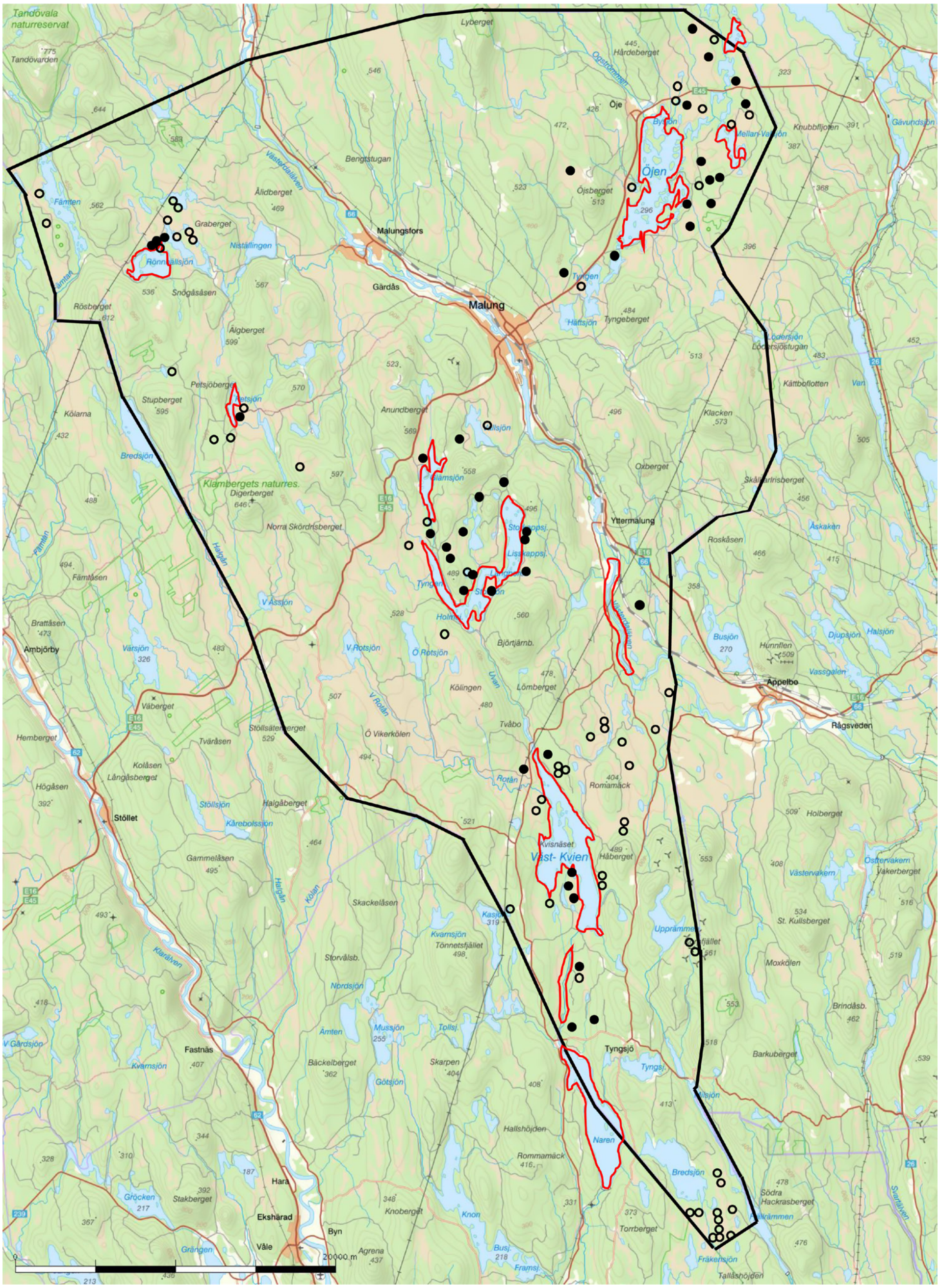

FIGURE 1. The study area. Filled circles=breeding pools included in this study, open circles=other pools with information about breeding Red-throated Loons *Gavia stellata* at least once during 1994–2019. Lakes and streams used for foraging by pairs breeding at pools included in this study are indicated with a red delimitation. The background map is downloaded from https://minkarta.lantmateriet.se/, with open access from The National Land Survey, © Lantmäteriet.

— Undersökningsområdet. Fyllda cirklar=häckningstjärnar som ingår i undersökningen, öppna cirklar=övriga tjärnar med information om häckande smålommar Gavia stellata *åtminstone en gång under perioden 1994–2019. Sjöar och vattendrag som nyttjas för födosök av par häckande vid tjärnar som ingår i undersökningen har markerats med röd avgränsning. Bakgrundskartan har laddats ner från https://minkarta.lantmateriet.se/, © Lantmäteriet.*

Material and methods

POOL HABITAT CHARACTERISTICS

For the purpose of this study, habitat characteristics were investigated at 41 pools (Figure 1, filled circles). A main criterion for the selection of pools was that data on the reproductive output should be available for at least six years, in accordance with recommendations for the monitoring of Common Loon *Gavia immer* populations in North America (Evers 2004). This criterion was met with reference to pool occupancy and for most pools included in the analyses of breeding success and chick survival (details in Appendices 1, 2 and 3).

The initial collection of data included 23 covariates (Table 1, for overview and further details), and we used a subset of these 23 covariates in statistical models. Subsequently, we assessed whether inclusion of additional covariates improved the predictive accuracies of our models, using a machine learning algorithm, as further explained under 'Statistical analyses.'

Surface area and shape of pool

Data was collected from official sources or measured on large-scale maps. The following covariates were included:

- Surface area (=A): Some previous studies have indicated that small pools (<1 ha) are more attractive for breeding or that pairs have a higher breeding success (Gomersall 1986, Okill & Wanless 1990, but not Eriksson & Johansson 1997, Skyllberg *et al.* 1999 or Dahlén & Eriksson 2002). Possible reasons for the inconsistent results are discussed by Dahlén & Eriksson (2002).
- Shore-length (=L): The primary reason for including this factor was for the calculation of the shoreline development index (below).
- Shoreline development index: $SLD=L/(2\sqrt{(\pi A)})$, as an indication of the spatial heterogeneity. $SLD=1$ for a circular pool, and larger for lakes and pools with an irregular shoreline and many islets. As mentioned above, Skyllberg *et al.* (1999) found that breeding success was correlated with an increasing mosaic character of the breeding pool.
- Maximum distance over open water: Take-off and landing require a minimum distance of open water (Norberg & Norberg 1971).

Occurrence of islets

Nests located on small islets have been assumed to be less susceptible for nest predation as well as human disturbance, and a higher breeding success has been reported in some studies (Lokki & Eklöf 1984, Skyllberg *et al.* 1999), but in contrast to e.g. Gomersall (1986) and Dahlén & Eriksson (2002). The diverging results might be related to the kind of predominating predators; if primarily mammal predators such as Red Fox, breeding on small islets might be adaptive, although it does not provide any protection against avian predators.

In this study the following covariates related to the number of islets were measured:

- Total number of islets.
- Total number of islets subjectively judged to be appropriate for breeding, with reference to gentle slope towards the water and easy access to any nest.
- Number of islets located more than 3 m from the shoreline; under the assumption that islets at that distance from the mainland shore are less easily accessible for mammalian predators, such as Red Fox.
- Number of islets located more than 3 m from the shoreline and subjectively judged to be appropriate for breeding.

Water throughflow

This covariate was included under the assumption that pools with well-defined inflow(s) and outflow are more exposed to water-level fluctuation and risk of flooded nests, e.g. after heavy rainfall. Contrary to expectation, Dahlén & Eriksson (2002) found indications that pools with through-flowing water were preferred for breeding and were more productive with reference to breeding success.

Cleared outlet

There is a historical tradition of draining wetlands and mires in order to create land for hay-making, also at sites located some distances from farms and settlements. In recent decades, drainage has been done in order to improve productivity in commercial forestry (Norstedt *et al.* 2021, for a recent study). In south-west Sweden, drainage has been found to be a reason for abandonment of breeding pools (Eriksson *et al.* 1988), although more recent field surveys indicate that shores and islets with a quagmire character may be recreated after some decades (Eriksson unpubl.).

TABLE 1. Methods for assessing the habitat characteristics included in the study. Covariates in parentheses were found to be correlated with other ones and excluded from the statistical analysis.
— Metoder för att bedöma de habitategenskaper som ingår i undersökningen. Variabler inom parentes befanns vara korrelerade med andra och uteslöts from de statistiska analyserna.

Covariates *Variabler*	Unit of measurement *Mätenhet*	Method and comments *Metod och kommentarer*
Area and shape of pools *Tjärnarnas areal och form*		
Surface area (=A) *Areal (=A)*	km^2	From official data sources or measured on large-scale maps. *Från officiella datakällor eller mätning på storskaliga kartor.*
(Shore length (=L)) *(Strandlängd, km)*	km	Measured on large-scale maps. Removed, correlated with ‘surface area’ and SLD. *Mätning på storskaliga kartor. Uteslöts, korrelerad med areal och flikighetsindex.*
Shoreline development index (SLD) *Flikighetsindex (SLD)*	see comments *se kommentar*	$L/(2\sqrt{(\pi A)})$
(Maximum distance over open water) *(Största avstånd över öppet vatten)*	m	Removed, correlated with ‘surface area’. *Uteslöts, korrelerad med areal.*
Occurrence of islets *Förekomst av småöar*		
Total number of islets *Totalt antal småöar*	number *antal*	Total count at site. *Totalräkning på plats.*
(As above but only those judged to be appropriate for nesting) *(Som ovan men endast de som bedömts lämpliga för häckning)*	number *antal*	Total count at site. Removed, correlated with ‘total number’ and subjective field assessment. *Totalräkning på plats. Uteslöts, korrelerad med totalt antal samt subjektiv bedömning i fält.*
Total number of islets, >3 m from the mainland shore *Totalt antal småöar, >3 m från fastlandsstranden*	number *antal*	Total count at site. *Totalräkning på plats.*
(As above but only those judged to be appropriate for nesting) *(Som ovan men endast de som bedömts lämpliga för häckning)*	number *antal*	Total count at site. Removed, correlated with ‘total number >3 m from the shore’ and subjective field assessment. *Totalräkning på plats. Uteslöts, korrelerad med totalt antal >3 m från stranden samt subjektiv bedömning i fält.*
Water throughflow *Genomströmmande vatten*	yes/no *ja/nej*	Checked at site. *Kontrollerat på plats.*
Cleared outlet *Rensat utlopp*	yes/no *ja/nej*	Checked at site. *Kontrollerat på plats.*
Distance to the most closely located freshwater used for foraging *Avstånd till närmast belägna sjö eller vattendrag som nyttjas för födosök*	km	Measured on large-scale maps. *Mätning på storskaliga kartor.*
Distance to road, manageable for 4WD vehicles *Avstånd till väg, körbar med fyrhjulsdrivet fordon*	m	Measured on large-scale maps. *Mätning på storskaliga kartor.*

TABLE 1 continued *fortsatt.*

Covariates *Variabler*	Unit of measurement *Mätenhet*	Method and comments *Metod och kommentarer*
Coverage and height of shoreline vegetation *Täckning och höjd av strandkantsvegetation*		
Sedges (Cyperaceae) and Water Horsetail *Equisetum fluviatile. Halvgräs och sjöfräken*	% coverage *% täckning*	Mean value of four transects, see text. *Medelvärde av fyra transekter, se texten.*
Bogbean *Menyanthes trifoliata. Vattenklöver*	% coverage *% täckning*	Mean value of four transects, see text. *Medelvärde av fyra transekter, se texten.*
(All vegetation) *(All vegetation)*	% coverage *% täckning*	Mean value of four transects, see text. Removed, correlated with 'Sedges and Water Horsetail'. *Medelvärde av fyra transekter. Uteslöts, korrelerad med 'halvgräs och sjöfräken'.*
(Average height of vegetation) *(Genomsnittlig höjd av vegetationen)*	cm	Mean value of four transects, see text. Removed, correlated with 'Sedges and Water Horsetail'. *Medelvärde av fyra transekter. Uteslöts, korrelerad med 'halvgräs och sjöfräken'.*
Sphagnum mosses *Vitmossor*	% coverage *% täckning*	Mean value of four transects, see text. *Medelvärde av fyra transekter, se texten.*
Vegetation in the water, 0–5 m zone along the mainland shore *Vegetation i vattnet, 0–5 m från fastlandsstranden*		
Standing/emergent vegetation *Stående vegetation*	% coverage *% täckning*	Mean value of four transects, see text. *Medelvärde av fyra transekter, se texten.*
Floating vegetation *Flytbladsvegetation*	% coverage *% täckning*	Mean value of four transects, see text. *Medelvärde av fyra transekter, se texten.*
(Total of above) *(Totalt av ovanstående)*	% coverage *% täckning*	Mean value of four transects, see text. Removed, correlated with 'floating vegetation'. *Medelvärde av fyra transekter, se texten. Uteslöts, korrelerad med flytbladsvegetation.*
Width of open mire belt around the pool *Bredd av öppet myrbälte kring tjärnen*		
Distance from shoreline to closest scrub *Avstånd från strandlinjen till närmaste buske*	m	Mean value of four transects, see text. *Medelvärde av fyra transekter, se texten.*
Distance from shoreline to closest tree *Avstånd från strandlinjen till närmaste träd*	m	Mean value of four transects, see text. *Medelvärde av fyra transekter, se texten.*
Proportion of quagmire along the shoreline *Proportionen gungfly utefter strandlinjen*	% proportion of shoreline *% proportion av strandlinjen*	Visually assessed at site. *Visuell bedömning på plats.*

Distance to freshwaters used for foraging

Distances from the central part of each pool to the shore of the most closely located freshwater used for foraging was measured on large-scale maps. This covariate was included under the assumption that foraging flights are energy-intensive, why this distance should be minimized. As mentioned in the introduction section, this aspect has been repeatedly investigated in previous studies, although the results are not entirely consistent.

Distance to road, drivable for 4WD vehicles

This covariate was included as an indication of accessibility by human visitors and risk of disturbance. However, no indications of any impact on the breeding success have been found in previous studies (Gomersall 1986, Dahlén & Eriksson 2002).

Coverage and height of vegetation around the pool

This aspect was investigated as we assumed that vegetation might provide nesting sites protected from predators. The coverage was measured within a zone of 0–5 m from the shoreline along four perpendicular transects pointing north, west, south and east from the approximate centre point of the pool. Coverage and maximum height of vegetation was estimated for each one of the five one-meter zones along each transect, giving a mean value for each transect, and the mean values of the four transects were the covariates used in the statistical analyses, as follows:

- Mean percentage coverage of sedges (Cyperaceae) and Water Horsetail *Equisetum fluviatile*.
- Mean percentage coverage of Bogbean *Menyanthes trifoliata*.
- Mean percentage coverage of all vegetation in the 0–5 m zone.
- Height of vegetation; assessed as average height along the same four transects.
- Mean percentage coverage of *Sphagnum* mosses.

Vegetation in the water

The percentage coverage of vegetation on the water, in a 5-m zone from the shoreline was visually assessed to the nearest 5% along the same four transects, using the mean values as the covariates used in the statistical analyses, as follows:

- Mean percentage coverage of emergent vegetation.
- Mean percentage coverage of floating vegetation.
- Mean percentage coverage of emergent and floating vegetation.

Width of open mire belt around the pool

Red-throated Loons require a minimum distance for take-off and landing, and arriving and leaving the pool by adult birds might be facilitated if it is surrounded by open land for pools where distance over open water is short. Distances from the shoreline to the nearest scrub and tree were measured along the same four transects as above, and mean values were used as covariates, as follows:

- Mean distance from shoreline to nearest scrub.
- Mean distance from shoreline to nearest tree.

Proportion of quagmire along the shore

Red-throated Loons place their nest very close to the shoreline with a slope that provides easy access to the water (Rizzolo *et al.* 2020); in the study area, as well as elsewhere in the Nordic countries primarily on quagmire (Rosenius 1942, Dahlén & Eriksson unpubl.). Thus, the percentage of quagmire along the mainland shore was assessed visually and used as a covariate.

An overview of the mean values, medians and ranges of the habitat characteristics is shown in Table 2 and primary data in the Appendices 4a and 4b.

The field work for assessing the habitat characteristics linked to coverage of vegetation was done during July–August 2018 and 2019. Thus, any long-term changes during the study period 1994–2019 were not picked up, which might have led to less accuracy of the assessments.

POOL OCCUPANCY AND REPRODUCTION

Three response variables related to the occurrence of Red-throated Loon and its reproductive output at various pools were investigated:

Pool occupancy

An obvious experience of the long-term surveys in the study area is that some pools were more frequently used by breeding Red-throated Loons than others. The criterion for deciding if a territory-holding pair was present or absent in a particular year was whether paired birds were observed at least twice with an interval of at least 15 days, unless breeding could be confirmed with records of eggs, incubating birds or pre-fledged chicks.

TABLE 2. Mean values, medians and ranges of habitat characteristics. Covariates in parentheses were found to be correlated with other ones and excluded from the statistical analysis. See Appendices 4a and 4b for primary data.
— Medelvärden, medianvärden och variationsbredd hos habitategenskaperna. Variabler inom parentes befanns vara korrelerade med andra och uteslöts from de statistiska analyserna. Se appendix 4a och 4b för primärdata.

Covariates *Variabler*	Mean *Medelvärde*	Median *Median*	Range *Variationsbredd*	Comments *Kommentarer*
Area and shape of pools *Tjärnarnas areal och form*				
Surface area (=A) *Areal (=A)*	0.010 km^2	0.007 km^2	0.001–0.041 km^2	<0.010 km^2 or 1 hectare for 27 of the 41 pools. *<0,010 km^2 eller 1 ha för 27 av de 41 tjärnarna.*
(Shore-length (=L) *(Strandlängd, km)*	0.55 km	0.52 km	0.20–1.64 km	
Shoreline development index (SLD) *Flikighetsindex (SLD)*	1.7	1.6	1.1–3.3	
(Maximum distance over open water) *(Största avstånd över öppet vatten)*	160 m	150 m	60–330 m	
Occurrence of islets *Förekomst av småöar*				
Total number of islets *Totalt antal småöar*	15	13	0–58	
(As above but only those judged to be appropriate for nesting) (*Som ovan men endast de som bedömts lämpliga för häckning)*	13	10	0–58	
Total number of islets, >3 m from the mainland shore *Totalt antal småöar, >3 m från fastlandsstranden*	2	1	0–12	
(As above but only those judged to be appropriate for nesting) *(Som ovan men endast de som bedömts lämpliga för häckning)*	2	1	0–12	
Water throughflow *Genomströmmande vatten*	see comment *se kommentar*	see comment *se kommentar*	see comment *se kommentar*	10 of the 41 pools. *10 av de 41 tjärnarna.*
Cleared outlet *Rensat utlopp*	see comment *se kommentar*	see comment *se kommentar*	see comment *se kommentar*	2 of the 41 pools. *2 av de 41 tjärnarna.*
Distance to the most closely located freshwater used for foraging *Avstånd till närmast belägna sjö eller vattendrag som nyttjas för födosök*	1.2 km	1.0 km	0.0–4.9 km	
Distance to road, manageable for 4WD vehicles *Avstånd till väg, körbar med fyrhjulsdrivet fordon*	0.3 km	0.2 km	0.1–0.8 km	

TABLE 2 continued *fortsatt.*

Covariates *Variabler*	Mean *Medelvärde*	Median *Median*	Range *Variationsbredd*	Comments *Kommentarer*
Coverage and height of shoreline vegetation *Täckning och höjd av strandkantsvegetation*				
Sedges (Cyperaceae) and Water Horsetail *Equisetum fluviatile. Halvgräs och sjöfräken*	10%	6%	0–40%	Predominantly sedges (*Carex* spp.). *Främst starr.*
Bogbean *Menyanthes trifoliata. Vattenklöver*	2%	1%	0–18%	<2% for 28 of the 41 pools. *<2% för 28 av de 41 tjärnarna.*
(All vegetation) *(All vegetation)*	14%	9%	1–57%	
(Average height of vegetation) *(Genomsnittlig höjd av vegetationen)*	13 cm	11 cm	1–40 cm	
Sphagnum mosses *Vitmossor*	8%	6%	0–30%	
Vegetation in the water, 0–5 m zone along the mainland shore *Vegetation i vattnet, 0–5 m från fastlandsstranden*				
Standing/emergent vegetation *Stående vegetation*	5%	5%	0–20%	<10% for 38 of the 41 pools. Predominantly sedges (*Carex* spp.), also small stands of Common Reed *Phragmites australis* and Water Horse-tail *Equisetum fluviatile* in single pools. *<10% för 38 av de 41 tjärnarna. Främst starr, men även smärre bestånd av bladvass och sjöfräken i vissa tjärnar.*
Floating vegetation *Flytbladsvegetation*	11%	5%	0–80%	<10% for 29 of the 41 pools. Predominantly water-lilies (*Nymphaea alba* and *Nuphar lutea*), also pondweeds (*Potamogeton* spp.) in single pools. *<10% för 29 av de 41 tjärnarna. Främst näckrosor men även nate i vissa tjärnar.*
(Total of above) *(Totalt av ovanstående)*	14%	5%	0–80%	
Width of open mire belt around the pool *Bredd av öppet myrbälte kring tjärnen*				
Distance from shoreline to closest scrub *Avstånd från strandlinjen till närmaste buske*	49 m	37 m	6–255 m	Primarily willow (*Salix* spp.) and Dwarf Birch *Betula nana* scrub *Främst buskage med viden och dvärgbjörk.*
Distance from shoreline to closest tree *Avstånd från strandlinjen till närmaste träd*	91 m	69 m	24–334 m	
Proportion of quagmire along the shoreline *Proportionen gungfly utefter strandlinjen*	87%	98%	10–100%	>70% for 33 of the 41 pools. *>70% for 33 av de 41 tjärnarna.*

Presence of a potential breeding pair, hereafter referred to as a *stationary pair*, was assessed for each pool, for each year with enough information for such an assessment.

Breeding success

For each stationary pair and year, we assessed breeding success as the presence or absence *of at least one large-sized chick*, being more than half of the length of an adult parent bird. In general, 2–4 visits at each breeding pool were required in order to get enough information for a reliable assessment. The first visit during each season was done before or during the nesting period, in order to reduce the risk of biased estimates due to undetected but failed breeding attempts. The timing of the last visit at each pool was adjusted in order to follow the survival of chicks until they were classified as large-sized or the absence of chicks was confirmed. Chicks of pairs not observed before or during the nesting period but only later during the season were not included in these assessments.

Chick survival

For successful pairs, we assessed the number of chicks as an index of the survival of pre-fledged chicks, in consistency with previous studies (Eriksson 2019). Most loon pairs lay two eggs (Dahlén & Eriksson 2002, with reference to the studied population) and the chicks' survival is primarily dependant on the parents' food provisioning success, as has been shown for the Red-throated Loon (Okill & Wanless 1990, Eberl & Picman 1993, Ball 2004, Rizzolo *et al.* 2014) as well as for the Black-throated Loon *Gavia arctica* (Jackson 2003). For these assessments we also included breeding attempts detected only during the chick rearing stage. While predation at the egg stage predominately leads to complete reproductive failure, the parents' foraging success affects the survival of chicks.

All the 41 pools were included in the analyses regarding pool occupancy and breeding success, while information was available for 39 pools with reference to chick survival.

STATISTICAL ANALYSES

General approach

The inclusion of correlated explanatory variables in models can lead to problems in the estimation of regression coefficients and in variable selection (Zuur *et al.* 2009). Thus, the initial step was to apply a commonly used threshold to reduce clusters of habitat variables with Spearman's rank correlation coefficient >|0.7| to one variable (Dormann *et al.* 2013). The following 16 habitat variables were retained: lake surface area, shoreline development index, total number of islets, total number of islets >3 m from the shore, water throughflow, cleared outlet, distance to foraging lake, distance to road, cover of sedges and horsetail, cover of bogbean, cover of sphagnum, cover of emergent vegetation, cover of floating vegetation, distance to closest scrub, distance to closest tree and proportion of quagmire along the shoreline (Table 1).

After the elimination of highly correlated variables, we fitted a generalized linear mixed model (GLMM) for each of the three response variables (below). Given the sample size of 39–41 pools, we limited the number of habitat covariates to four to avoid problems in the estimation of regression coefficients and variances (Peduzzi *et al.* 1996). Then, we evaluated if the inclusion of additional covariates reduced prediction error of models, using the machine learning algorithm random forest (Breiman 2001, see below). In contrast to most regression-based approaches, random forest is robust to a large number of covariates relative to the sample size, which enabled us to include all 16 habitat covariates (Grömping 2009). The analysis was carried out in R v.4.0.3 (R Core Team 2020).

Generalized linear mixed model

We modelled (1) the probability of a pool being occupied by Red-throated Loon, (2) the probability of pairs successfully producing large young and (3) the probability of successful pairs producing two large young. For each response variable, we fitted a generalized linear mixed model using a Bernoulli distribution and a logit link. We split reproduction into two models because this allowed us to include data on chick survival when breeding attempts were discovered during the chick rearing phase. With this approach we could distinguish between habitat characteristics leading to complete reproductive failure and habitat characteristics influencing chick survival, reflecting that predation at the egg stage predominately leads to complete reproductive failure, while limited food availability may lead to fewer fledglings.

We accounted for repeated observations of the same pools in several years by fitting pool and year as random intercept terms. Continuous covariates were standardized to a mean of zero and a standard deviation of one before model fitting. Models were fitted with package glmmTMB using maximum likelihood estimation and the Laplace approximation (Brooks *et al.* 2017). Functions from package DHARMa (Hartig 2018) facilitated in verifying the validity of the assumptions of our generalized linear mixed models. To assess residual temporal and spatial autocorrelation of model residuals, we carried out Durbin-Watson tests and calculated Moran's I autocorrelation coefficient.

We fitted the following habitat covariates as fixed effects:

1. Pool surface area because some previous studies found that smaller pools were preferred by Red-throated Loon or were associated with a higher breeding success.
2. Distance to foraging lake as we expected that breeding pools closer to foraging lakes would be energetically advantageous to Red-throated Loon and consequently might be preferred and/or lead to a higher reproductive performance.
3. A measure of the extent of the open mire belt as our study area was in a forested landscape and the extent of the open mire belt may therefore be important to facilitate take-off and landing of the species. Consequently, we expected that the extent of the open mire belt might influence pool selection by Red-throated Loon and reproductive performance.
4. One of the measures of spatial heterogeneity/vegetation cover. Among the covariates shoreline development index, cover of sedges and horsetail, cover of bogbean, cover of sphagnum, cover of emergent vegetation and cover of floating vegetation we chose cover of floating vegetation, speculating that cover of floating vegetation might benefit the survival of chicks and consequently might affect pool selection by Red-throated Loon. We included the cover of floating vegetation only in the model for pool occupancy and chose an alternative fourth covariate for the reproduction models.
5. Cleared outlet in the reproduction models as drainage can affect the whole pool environment. Additionally, this habitat covariate can be more easily impacted through conservation management than several others in our dataset and is therefore of particular interest. As the occurrence of cleared outlets was not very prevalent in the study area reducing our chances of detecting an effect, we limited the inclusion of this covariate to the reproduction models.

The remaining covariates, distance to road, water throughflow, the alternative measure of the extent of the open mire belt, alternative measures of spatial heterogeneity and vegetation cover and measures of the availability of nesting opportunities (total number of islets, total number of islets >3 m from the shore, proportion of quagmire) were evaluated only via the random forest models.

For *pool occupancy* we modelled presence or absence of Red-throated Loon at 41 pools 1994–2019 (569 presences and 146 absences). As a measure of the extent of the open mire belt, we chose distance to nearest tree. All four habitat covariates were included as fixed effects. We log transformed lake area, distance to foraging lake and distance to nearest tree as this improved the residual diagnostic plots of the model. As an additional fixed effect, we fitted Year as a continuous variable to account for a possible temporal trend in local population size, which could affect occupancy.

For *breeding success* we modelled whether pairs successfully produced young (41 pools, 1994–2019, 279 successful and 262 unsuccessful breeding attempts), having in mind that the same pair might have been included repeatedly as most pools were surveyed in several years. Initially we chose distance to nearest tree as the measure of the extent of the open mire belt as in the model on pool occupancy. However, plots of model residuals over the alternative measure, distance to nearest scrub, indicated a possible pattern. Pattern in the residual plots could indicate a potential omission of an important covariate and hence a potential misspecification of the model (Zuur *et al.* 2009). Therefore, we chose the distance to nearest scrub as the measure for the extent of the open mire belt.

For *chick survival* we modelled whether successful pairs produced two young or not. Therefore, this model estimated the probability of successful pairs producing two chicks instead of one (39 pools, 1994–2019, 217 nesting attempts producing one young and 85 attempts producing two young). We fitted the same measure for the extent of the open mire belt used in the model on breeding success: distance to nearest scrub.

Model selection and validation

We applied model selection to each of our three GLMMs to obtain parsimonious models that balance goodness of fit with model complexity. We used Akaike's information criterion (AIC) for model selection, a commonly used method (Burnham & Anderson 2004, Zuur *et al.* 2009). The AIC describes the certainty of a model being the best one among a set of candidate models. For each response variable, our set of candidate models consisted of the model described above and all possible nested models (all possible combinations of the fixed effects). We calculated AICc (Akaike's information criterion for small samples), which is recommended unless sample sizes are large (Burnham & Anderson 2004). Often there is considerable uncertainty which of several models is the best one (Symonds & Moussalli 2011), and Akaike weights facilitate in the assessment of the strength of a candidate model relative to the best model (the model with the lowest AICc). Akaike weights are calculated using the differences in AICc between candidate models and the model with the lowest AICc (ΔAICc henceforth), and they can be interpreted as representing the probability that a candidate model is the best one (Symonds & Moussalli 2011).

We ranked all models in ascending order by their AICc and present all models with a cumulative Akaike weight ≤0.95, which can be interpreted as the set of models containing the best model with 95% confidence (Symonds & Moussalli 2011). We also present predictor weights, which are the sum of Akaike weights of all models containing a given covariate. Predictor weights can be interpreted as representing the probability of a given covariate being in the best model (Symonds & Moussalli 2011). Predictor weights ≥0.4 suggest that the covariate may be important and the closer the value is to 1, the more support for the conclusion that a covariate is important (Burnham 2015). We calculated AICc and Akaike weights using R package MuMIn (Barton 2020).

One aim of our study was to explore relationships between the response variables and important covariates. We visualized the species-habitat associations for habitat covariates with predictor weights ≥0.4. This relatively low predictor weight threshold ensured a low probability of erroneously not considering important covariates. Predicted probabilities were plotted over the range of observed values for each habitat covariate. Values for fixed effects other than the focal fixed effect were set to the mean value in the observed data. We predicted using only the fixed effects, i.e. for an average pool and year in the study population. We present graphs of species-habitat relationships based on models with all covariates that exceeded our chosen predictor weight threshold of 0.4. Graphs of species-habitat relationships based on full models or on model averaging were very similar and are not presented.

We also calculated the theoretical coefficient of determination R^2_{GLMM} (Nakagawa *et al.* 2017) using package MuMIn for the ΔAICc=0 model and additionally for the model with all habitat covariates with predictor weights ≥0.4. We calculated the proportion of the total variance explained by the fixed effects (marginal R^2_{GLMM}) and the proportion of the total variance explained by both the fixed and random effects (conditional R^2_{GLMM}).

Cross-validation of predictive models

A second aim of our study was to evaluate if we could reliably predict pool occupancy or reproductive performance of Red-throated Loon based on pool habitat characteristics. Balancing goodness of fit with model complexity is important for prediction as models can fit to local heterogeneity or noise when unnecessary covariates are included and consequently will be less generalizable, resulting in larger prediction errors with new data (Wenger & Olden 2012). We therefore chose the ΔAICc=0 models for prediction, in contrast to our model explorations above, where we considered all covariates with predictor weights ≥0.4. Predicting on the same data used for model fitting and comparing predicted versus observed data can result in overoptimistic evaluations of predictive accuracy of models (Bahn & McGill 2013). Therefore, we used leave-one-out cross-validation to evaluate how well our models predicted pool occupancy or chick survival. We did not apply cross-validation to the breeding success model because breeding success was poorly explained by the fixed effects (below) and thus the model was not useful for predicting breeding success based on habitat characteristics of pools. We withheld data from all years for a pool and fitted the model with the data from the remaining pools. Based on the habitat characteristics of the pool that was withheld, we then used the model to predict pool occupancy or chick survival for the pool for each year. We repeated this process until all pools were withheld once. Subsequently, we calculated mean predicted occupancy or chick survival for each pool across all years. Then, we compared the predicted versus the observed data by fitting a linear model of the mean predicted probabilities per pool versus the proportion of years each pool was observed as occupied, or the proportion of years successful pairs raised two young. We also calculated prediction intervals, which are an estimate of the interval in which a new pool from the same population of pools will fall.

Random forest models

We built our generalized linear mixed models with a small number of habitat covariates that we expected to be most relevant for each response variable. However, ecological knowledge of most species is incomplete and such pre-selection of covariates carries the risk of not evaluating covariates that may in fact affect the species. We identified and measured 16 covariates which may potentially affect pool occupancy by Red-throated Loon or reproduction. Using the machine learning algorithm random forest, we evaluated if additional variation in our response variables was explained by including all 16 habitat covariates instead of only the habitat covariates with predictor weights ≥0.4.

Briefly, random forest consists of many regressions or classification trees combined in an ensemble (Breiman 2001). Each of the many trees in the forest is grown on a random selection, usually ⅔, of the data. Available predictors at each node split are randomly selected which introduces additional randomisation and a diverse ensemble of trees, which can result in more accurate predictions of the response variable (Breiman 2001, Liaw & Wiener 2002, Strobl *et al.* 2009). Each tree is used to predict the data not used in the construction of the tree, the Out-of-bag or OOB data. The majority vote of all predictions for each datapoint is used to produce an average prediction. The OOB error is the proportion of datapoints for which this average prediction is not the same as the true class (Liaw & Wiener 2002).

For each response variable, we calculated the OOB error when including all 16 habitat covariates and separately when including only the habitat covariates with predictor weights above our threshold of 0.4. Sample sizes were the same as in the GLMMs. Due to the randomness in the algorithm, OOB errors vary slightly between repetitions of a random forest model. Therefore, we repeated each random forest model ten times. Subsequently, we evaluated if models with all 16 habitat covariates reduced OOB error compared to the models with the smaller set of covariates by fitting a linear regression with OOB error as the response variable. The single explanatory variable was a factorial covariate with two levels: inclusion of all 16 habitat covariates or inclusion of the smaller set of habitat covariates identified by the generalized linear mixed models.

We used R package randomForest (Liaw & Wiener 2002) and default settings with the following exceptions: (1) we increased the number of trees in the ensemble from the default number of 500–2,000, which increases the stability of the results, (2) for the random forest models on pool occupancy (569 presences, 146 absences) and number of young (217 pairs with one chick, 85 pairs with two chicks), we randomly down-sampled the larger class (presences/pairs with one chick) to match the size of the smaller class (146 and 85 respectively), which better balances the error rates between the smaller and the larger class (Chen *et al.* 2004). Therefore, each of the 2,000 classification trees in a forest was grown on a down-sampled random sample of data. Otherwise, error rates of the larger class (here presences and pairs with one chick) would be minimized at the expense of error rates of the smaller class, here absences and pairs with two chicks.

Results

OCCUPANCY OF POOLS AND REPRODUCTION

The average occupancy among the 41 pools included in this study was 79% (SD±15%) per year during the study period 1994–2019, and we never recorded more than one stationary pair in any of the pools during the study period (primary data in Appendix 1). The mean breeding success was 0.66 (SD±0.18) large-sized chicks per stationary pair and year, and the mean percentage of broods with two large-chicks was 28% (SD±15%) per year (primary data in Appendices 2 and 3). Thus, the reproductive output was similar to that for South-central Sweden as a whole during the period 1994–2018;

e.g. 0.60 (SD±0.15) large chicks per pair and year, and an average percentage of broods with two large-chicks was 30% (SD±9%) per year (Eriksson 2019).

HABITAT CHARACTERISICS

Pool occupancy

The set of models containing the best model with 95% confidence included 13 models (Appendix 5). Akaike weights per model were low (max: 0.156) indicating considerable uncertainty in identifying the best model. Predictor weights for all habitat covariates were ≥0.4, a threshold for consideration as possible important covariates. Good support was obtained for the two covariates percentage of floating vegetation (predictor weight: 0.767) and lake area (predictor weight: 0.641) with lower support for distance to foraging lake (predictor weight: 0.472) and distance to tree (predictor weight: 0.451). The predicted probability of a pool being occupied increased when the percentage of floating vegetation was higher, the pool was smaller and the foraging lake and the nearest tree closer (Table 3, Figure 2, Appendix 5). The coefficient of determination R^2_{GLMM} for the model including all fixed effects with predictor weights ≥0.4 (ΔAICc=0.252) was 0.303 (marginal) and 0.530 (conditional). In other words, 30.3% of the variance in pool occupancy was explained by the fixed effects (four habitat covariates and year) in the model and 53.0% of the variance in pool occupancy was explained by both the fixed and the random effects. Variability between pools was larger than between years (SD for random effect Pool: 1.095, and for random effect Year: 0.621). The ΔAICc=0 model included the fixed effects floating vegetation, lake area and year. The R^2_{GLMM} of the ΔAICc=0 model was 0.277 (marginal) and 0.531 (conditional).

Based on cross-validation and the model with ΔAICc=0, the mean predicted occupancy probability per pool across years was positively associated with the proportion of years pools were observed as occupied (Figure 3, left, regression coefficient=0.288, SE=0.077, $p<0.001$, $R^2=0.248$).

Breeding success

The set of models containing the best model with 95% confidence included 14 models (Appendix 6) and the ΔAICc=0 model contained none of the habitat covariates (Table 3). Akaike's weights per model were low (max 0.134) indicating considerable model selection uncertainty. Only two covariates exceeded the threshold of 0.4 for predictor weights indicating that breeding success may be higher if scrubs are farther away or the pool is smaller (Table 3, Appendix 6). However, both predictor weights were near 0.4, indicating only very low support for these possible relationships (distance to scrub: 0.431; lake area: 0.403). For the model with both covariates with predictor weights ≥0.4, (ΔAICc=1.235), only 2.0% of the variance in breeding success was explained by the fixed effects while 17.3% of the variation was explained by both the fixed and random effects (R^2_{GLMM}: 0.020 (marginal) and 0.173 (conditional) with the conditional R^2_{GLMM}=0.176 for the ΔAICc=0 model). Variability in breeding success between years was close to zero while the model showed larger variability between pools (SD for random effect pool: 0.778, and for random effect Year: 0.0001). Due to the low support for the influence of any of the four habitat covariates on breeding success, we do not present plots to visualize the possible relationships.

Chick survival

The set of models containing the best model with 95% confidence included eight models (Appendix 7). As in the previous two analyses, Akaike weights per model were low (max: 0.226) indicating considerable uncertainty in identifying the best model. Predictor weights for distance to foraging lake was high (0.934) and inclusion of distance to scrub was also supported (predictor weight: 0.541). Predictor weight for the covariate cleared outlet was near the 0.4 threshold (0.397) and no support was found for lake area (predictor weight: 0.272). The probability of a successful pair producing two young increased when the foraging lake was closer and the nearest scrub farther (Table 3, Figure 4, Appendix 7). For the model including habitat covariates with predictor weights above 0.4 (ΔAICc=0), 8.6% of the variation was explained by the two fixed effects and 21.7% by both the fixed and the random effects (marginal R^2_{GLMM}=0.086, conditional R^2_{GLMM}=0.217). Variability between years was slightly larger than between pools (SD for random effect pool: 0.470, and for random effect Year: 0.576).

For pairs raising at least one chick and based on cross-validation and the model with ΔAICc=0, predicted chick survival was positively associated with

TABLE 3. Predictor weights of covariates and regression coefficients with SE in full and best (ΔAICc=0) models for the three response variables. All covariates were standardized to a mean of zero and a standard deviation of one before model fitting. In the pool occupancy model, regression coefficients apply to log-transformed values for pool surface area, distance to foraging lake and distance to tree.
— Variabelvikter för habitatvariabler och regressionskoefficienter med standardfel (SE) för habitatvariabler för kompletta och bästa modeller för de tre responsvariablerna. Alla habitatvariabler standardiserades till ett medelvärde=0 och en standardavvikelse=1 innan de lades in i modellen. För modellen avseende nyttjande av häckningstjärnar avser regressionskoefficienten log-transformerade värden för areal, avstånd till fiskevatten och avstånd till närmaste träd.

	Pool occupancy *Nyttjande av tjärnar*			Breeding success *Häckningsframgång*			Chick survival *Ungarnas överlevnad*		
	Predictor weight *Variabelvikt*	Full model *Komplett modell*	Best model *Bästa modell*	Predictor weight *Variabelvikt*	Full model *Komplett modell*	Best model *Bästa modell*	Predictor weight *Variabelvikt*	Full model *Komplett modell*	Best model *Bästa modell*
ΔAICc		0.252	0		3.790	0		2.916	0
Intercept *Intercept*		2.030±0.276	2.025±0.285		0.076±0.158	0.013±0.166		−1.097±0.221	−1.152±0.222
Pool surface area *Areal*	0.641	−0.486±0.249	−0.415±0.221	0.403	−0.140±0.150		0.272	0.082±0.160	
Distance to foraging lake *Avstånd till fiskevatten*	0.472	−0.414±0.273		0.347	−0.150±0.157		0.934	−0.546±0.196	−0.480±0.189
Distance to scrub *Avstånd till buskage*				0.431	0.182±0.172		0.541	0.242±0.168	0.271±0.170
Distance to tree *Avstånd till träd*	0.451	−0.476±0.276							
Floating vegetation *Flytande vegetation*	0.767	0.539±0.242	0.524±0.253						
Cleared outlet *Rensat utlopp*				0.366	−0.678±0.661		0.397	−0.841±0.797	
Year *År*	1.000	−1.157±0.208	−1.172±0.209						

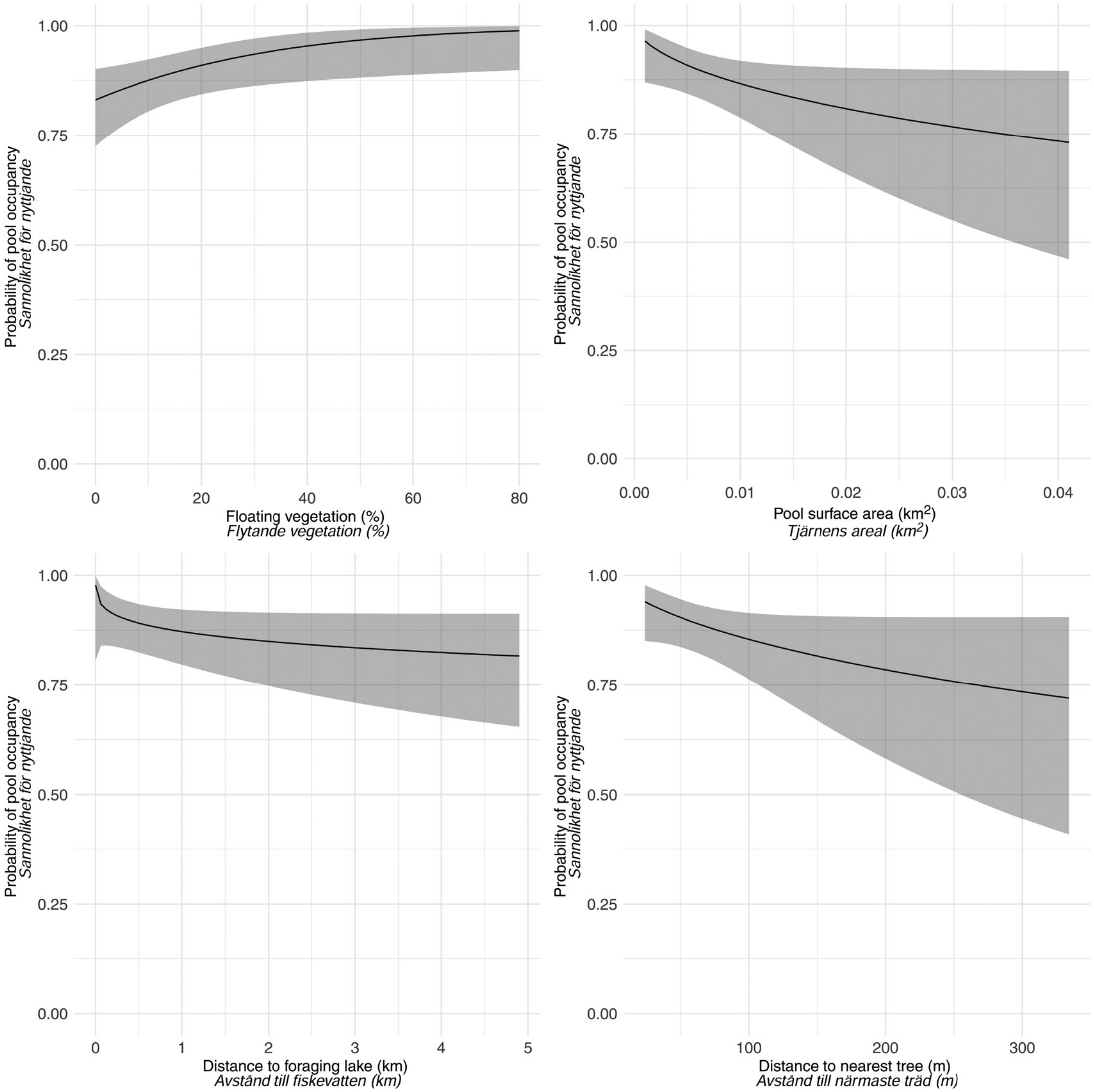

FIGURE 2. The predicted mean probability of pool occupancy and the 95% confidence interval for each of the four covariates floating vegetation, pool surface, distance to foraging lake and distance to nearest tree. For each plot, values of all other covariates were fixed to the mean value in the observed data. Predictions were based on the estimates of regression coefficients of the model with all covariates above our chosen threshold for predictor weights ≥0.4 (full model in Table 3).

— Den predikterade genomsnittliga sannolikheten för nyttjande av en häckningstjärn, med 95% konfidensintervall för de fyra variablerna flytande vegetation, tjärnens areal, avstånd till närmaste fiskevatten och avstånd till närmaste träd. För varje graf har värdena för alla övriga variabler fixerats till medelvärdet av observerade data. Prediktionerna baserades på modellen med alla habitatvariabler över tröskelvärdet för variabelvikten, ≥0,4 (komplett modell i tabell 3).

observed chick survival. (Figure 3, right, mean predicted probability of pairs raising two chicks modelled as a function of the observed proportion of years in which two chicks were raised: regression coefficient=0.178, SE=0.073, p=0.021, R^2=0.113).

All habitat covariates

Random forest models with all 16 habitat covariates did not achieve lower OOB error rates compared to random forest models with habitat covariates with predictor weights ≥0.4 for any of the three models (all p≥0.10).

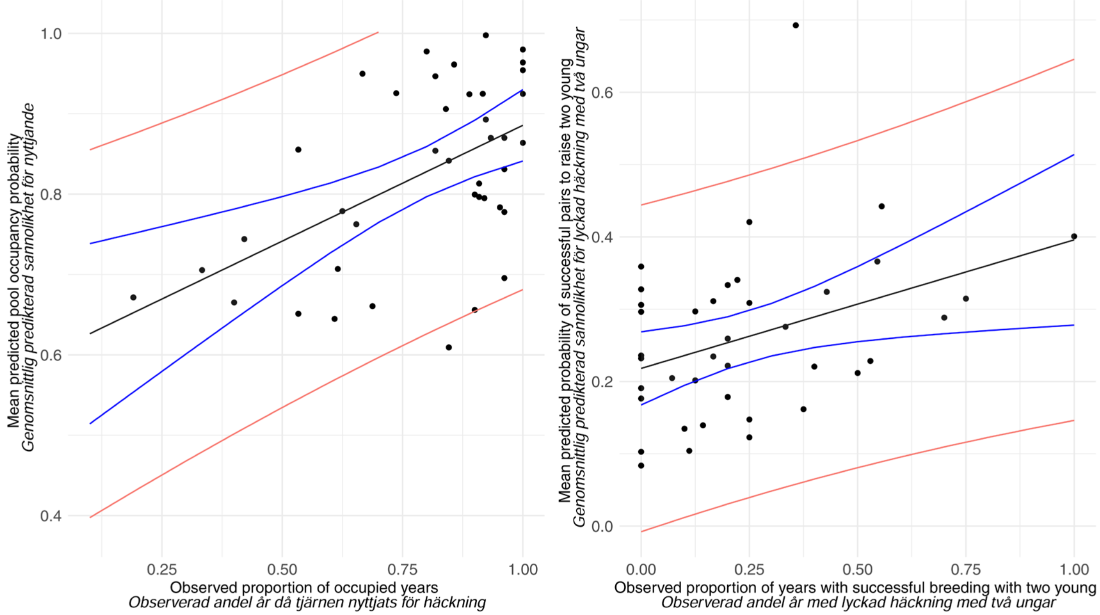

FIGURE 3. Scatterplot of predicted versus observed data with regression line (black), the 95% confidence interval (blue) and the 95% prediction interval (red). Left: cross-validated mean predicted occupancy probabilities per pool versus the observed proportion of years occupied. Right: cross-validated mean predicted probabilities per pool of a Red-throated Loon pair to raise two young in years with breeding success versus the observed proportion of years with breeding success in which two young were raised. For a new dataset of pools in the study area, there is a 95% chance that the regression line will fall within the blue 95% confidence interval, and for a new pool in the study area there is a 95% chance that it will fall within the red 95% prediction intervals.
— Spridningen av förutsedda kontra observerade data med regressionslinje (svart), 95% konfidensintervall (blått) och 95% prediktionsintervall (rött). Vänster: Korsvaliderade genomsnittliga predikterade sannolikheter per häckningstjärn i relation till den observerade andelen år då tjärnen nyttjades för häckning. Höger: Korsvaliderade genomsnittliga predikterade sannolikheter per häckningstjärn för att ett smålomspar ska föda upp två ungar under ett år med lyckad häckning i relation till den observerade andelen år med lyckad häckning med två ungar. För ett nytt dataset med tjärnar i undersökningsområdet är chansen 95% att regressionslinjen faller inom det blåa 95% konfidensintervallet, medan det för en enstaka ny tjärn i undersökningsområdet är en 95% chans att den faller inom det röda 95% prognosintervallet.

Discussion

HABITAT CHARACTERISTICS SUPPORTED BY THE MODELS

We found good support for the conclusion that smaller pools and a greater coverage of floating vegetation were preferred by Red-throated Loon pairs, and lower support for a preference of pools closer to foraging lakes and closer to the forest edge. We also found good support for the conclusion that successful pairs raised more chicks at pools closer to foraging lakes and surrounded by a wider mire belt, as further elaborated below. However, we found little support to suggest that breeding success was affected by the habitat variables we investigated.

Due to the high model selection uncertainty in each of the three generalized linear mixed models, we based the evaluation of associations between habitat characteristics and each of the three response variables on predictor weights (Table 3, for overview). For the model on breeding success, the only two habitat covariates with predictor weights above the 0.4 threshold were distance to nearest scrub, suggesting a possible positive effect of a wider mire belt, and pool surface area, suggesting the possibility that smaller pools were associated with greater breeding success. However, the low predictor weights suggest low support for these possible relationships. A likely reason is an overall high nest predation pressure that was not explained by the habitat covariates in the models, having in mind that predation is a major reason for nesting failures in this study area (Dahlén & Eriksson 2002), as well as for Red-throated Loon populations studied elsewhere (Eberl & Picman 1993, Skyllberg *et al.* 1999, Hulka 2010, Rizzolo *et al.* 2014, Olsson *et al.* 2021).

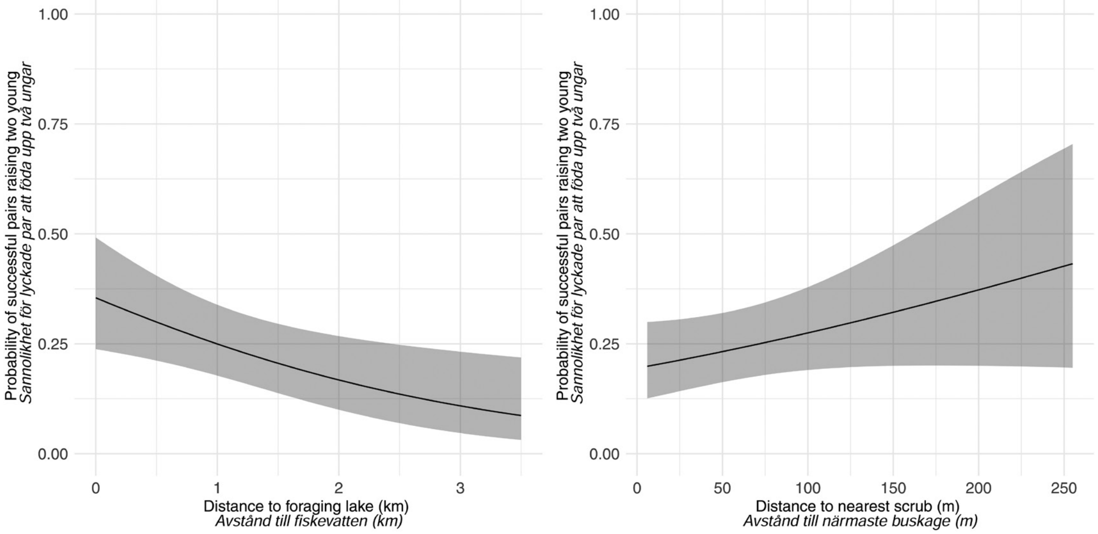

FIGURE 4. The predicted probability and the 95% confidence intervals of successful pairs producing two young for the two habitat covariates distance to foraging lake and distance to nearest scrub. For each plot, values of the other covariate were fixed to the mean value in the observed data. Predictions were based on the estimates of regression coefficients of the model with all covariates above our chosen threshold for predictor weights ≥0.4 (best model in Table 3).
— Den predikterade sannolikheten för att par med lyckad häckning producerar två ungar, med 95% konfidensintervall för de två variablerna avstånd till fiskevatten och avstånd till närmaste buskage. För varje graf har värdena för alla övriga variabler fixerats till medelvärdet av observerade data. Prediktionerna baserades på modellen med alla habitatvariabler över tröskelvärdet för variabelvikten, ≥0,4 (komplett modell i tabell 3).

Our results are not entirely consistent with those in a previous study in the same area during 1991–2000 (Dahlén & Eriksson 2002). In that study, and with reference to univariate regressions, no indications of relationships between surface area or distance to closest foraging water were found, neither with pool occupancy nor breeding success. There were, however, weak but significant negative univariate correlations between these habitat characteristics and the percentage of broods with two large chicks (Table 10 in Dahlén & Eriksson 2002).

The surface areas of the pools ranged over 0.1–4.1 ha, and 27 (66%) of them were smaller than 1 ha (Table 2). The smallest pools were the ones being most frequently occupied and they might have experienced a higher breeding success, in consistency with findings in some previous studies in Shetland (Gomersall 1986, Okill & Wanless 1990).

Although the Red-throated Loon has a wide geographic range where it demonstrates some flexibility in foraging strategies during the breeding season, the location of nest sites in relation to appropriate foraging waters remains a constraint (Duckworth *et al.* 2021). Most likely, Red-throated Loon parents feeding chicks are under physiological stress, why selection of breeding pools on short distance to the foraging waters might be rewarding. The energy requirements only for take-off and climbing does not leave much extra margin for carrying fish placed crosswise in the bill to a breeding pool located at some distance (Norberg & Norberg 1976), and the chick rearing strategy has been proposed to be adapted to reducing the number of food provisioning trips (Rizzolo *et al.* 2015). Thus, the issue of travelling distance between breeding pool and foraging waters has been handled in several previous studies, but the results are not entirely consistent. Some studies indicate that the breeding success is independent of the distance to foraging waters up to 8–9 km where the frequency of foraging flights and thus the survival of the chicks might be affected (Merrie 1978, Eberl & Picman 1993, Douglas & Reimchen 1988). However, the 41 breeding pools included in the present study were located over a smaller range from very close to the foraging waters (zero in the statistical models) up to 4.9 km, and nevertheless we got good support for the conclusion that successful breeding pairs also managed to rear two chicks more frequently at pools located close to foraging freshwaters. Furthermore, there was an indication that these pools might have been occupied more frequently. Short distance between the breeding pool and foraging lake makes more frequent flights possible at a similar energetic cost in comparison to alternative breeding at pools located more distantly, and hence a more cost-effective fish delivery that might help to enhance the survival of the chicks.

There was also support for the occurrence of floating vegetation as a habitat characteristic that makes pools attractive for breeding. Among the 41 pools, water-lilies (*Nymphaea alba* and *Nuphar luteum*) are predominant, although pondweed (*Potamogeton* spp.) is also found but less frequently. This vegetation is not visible on the water-surface when the birds arrive in spring or when they start breeding, but has developed at the time when non-fledged chick are present. Speculatively, floating vegetation might contribute to a higher spatial heterogeneity, to the benefit for the chicks' survival, e.g. in terms of protection against predators. Having in mind that loons are long-lived species, they might have memorised any occurrence from previous seasons, if floating vegetation indicates any important habitat quality.

The outcome of the models indicated low support for higher breeding success, but better support for higher survival of the pre-fledged chicks at pools with a longer distance from the shoreline to the nearest scrub (Table 3), within a range of 6–255 m (Table 2). Thus, Red-throated Loon pairs might benefit from an extensive area of open land around the pool. Having in mind that the attraction to small-sized breeding pools may result in short distance over an open water surface for take-off and landing, this disadvantage may be compensated by the extent areas of open land around the pool. In practise and with reference to the management of breeding pools for Red-throated Loon in the Nordic countries of Europe, 'open land' mostly is similar to 'open mire'.

However, for occupancy of pools, there was weak support for a negative relationship between closeness to trees around the pool and occupancy (Table 3), with a range of 24–334 m from the shoreline to the nearest tree among the 41 pools (Table 2). This finding contradicts our expectations, with reference to previous perceptions of open mires as an important breeding habitat, although our result indicates a preference for pools surrounded by forest. The result might just be dismissed with reference to low predictor weight (0.451), but if of any substance it might indicate that the common idea of Red-throated Diver as primarily belonging to the bird fauna of open mires might reflect biased observations, so far as loons breeding on open mires might be easier to detect than those breeding at pools surrounded by forest during field surveys. Speculatively, the 'ideal' combination for breeding might be a pool located in a forested area but with a zone of open mire surrounding the pool.

ADDITIONAL HABITAT CHARACTERISTICS

The subsequent evaluation, using the random forest algorithm, showed that using all covariates did not improve the ability to predict pool occupancy, breeding success and the successful rearing of two chicks, compared to models based on habitat covariates with predictor weights ≥0.4. But this does not rule out that another combination of covariates than those initially chosen in the generalized linear mixed models would alternatively be able to predict pool occupancy etc., at least to some extent. Thus, we briefly discuss the current knowledge of associations between Red-throated Loon and a mosaic distribution of open water and vegetation, the number of islets, water throughflow and distance to roads.

Skyllberg *et al.* (1999) found that breeding success was higher at pools with a mosaic of open water and vegetation which was thought to provide nest sites safe from predation. However, similar comparatively large-sized pools with a mosaic distribution of vegetation and islets, were lacking in our study area.

Dahlén & Eriksson (2002) found no association between Red-throated Loon pool occupancy or breeding success and the number of islets at a pool. However, higher breeding success at pools with many islets has been reported in some other studies (Lokki & Eklöf 1984, Skyllberg *et al.* 1999). Possible reasons for different results between various studies may be related to the predominating predators, as discussed in some detail by Dahlén & Eriksson (2002).

In the previous study during 1991–2000, pools with flowing-through water were found to be more attractive for breeding Red-throated Loons, and pairs at such pools had higher breeding success (Dahlén & Eriksson 2002). Earlier findings, such as Eriksson *et al.* (1988) for south-west Sweden suggest that drainage may have a long-term negative impact on Red-throated Loon.

Including the distance to road drivable by 4WD vehicles additionally to covariates with predictor weights ≥0.4 did not lead to more accurate predictions of the occupancy of pools, breeding success or the survival of pre-fledged chicks, again consistent with the study from 1991–2000 (Dahlén & Eriksson 2002). However, none of the 41 pools were located remotely with reference to distance from a drivable road, and the range of 0.1–0.8 km might be too small to expect any difference in impact. In addition, breeding pairs may habituate to human presence (Nummi *et al.* 2013).

Finally, it should be considered that the parents' physical condition might affect the reproductive performance or if to initiate breeding in a particular season (Drent & Daan 1980); the latter an issue of relevance for long-lived species such as the Red-throated Loon. For example, it has been proposed that exposure to various threats in marine wintering sites might affect the survival of Red-throated Loons breeding in Alaska (Schmutz 2014). Furthermore, fluctuations between years in the reproductive performance by the Swedish population are synchronised between different parts of the country, which might indicate geographically large-scale impact during other parts of the annul cycle than the breeding season (Eriksson 2019). The random intercept terms of year and pool in our models can account for variation between years and between pools, including variation between pools that may be due to differences in the quality of breeding pairs.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Based on the analyses, we identified three habitat characteristics of importance for the conservation and management of Red-throated Loon populations that inhabit the inland coniferous forest landscape of the Nordic countries of Europe: Surface area of pools, distance between breeding sites and freshwaters used for foraging and the extent of open mire around the pool. If to generalize, the ideal breeding pool should be small, located close to freshwaters appropriate for foraging, and surrounded by open mire in a forested landscape. High coverage of floating vegetation might be an additional habitat quality, but only possible to map during field surveys quite late in the breeding season.

Thus, the management of an inland breeding Red-throated Loon population must adopt a landscape perspective, taking both breeding sites and foraging waters into account, as well as the flight corridors between them. Hitherto, the management has primarily been focussed on the breeding sites, while less emphasis has been given to the foraging waters. At least two aspects must be considered: (1) the fish fauna in alternative freshwaters for foraging and (2) the distance between breeding pools and these freshwaters.

Although Red-throated Loon and the sympatric Black-throated Loon often forage in the same lakes, there are overall differences in water chemistry and the composition of the fish communities; pH and alkalinity are on average lower in the lakes used for foraging by Red-throated Loons (Eriksson & Paltto 2010). Red-throated Loons forage within a narrower and more 'exclusive' spectrum of lakes, with a focus on waters with abundant stocks of small-sized cyprinid or salmonid fish, <20 cm length. These kinds of fish dominate among the prey delivered to the young (Eriksson *et al.* 1990), and there are positive relationships between the abundance of them and the survival of pre-fledged chicks (Figure 3 in Eriksson 2006). A recent study of the diet of piscivorous bird species in 36 lakes in northern Sweden further confirmed the importance of *Coregonus* species for the Red-throated Loon (Söderlund 2020).

Thus, identification and the appropriate management of freshwaters with abundant stocks of prey fish must be an important cornerstone in the management of Red-throated Loon populations. In practice, this means freshwaters with stocks of small-sized Vendace *Coregonus albula* or Whitefish *Coregonus lavaretus* for most waters used for foraging in the Nordic countries of Europe (Eriksson 2006, Eriksson & Paltto 2010, Söderlund 2020). These are fish with high energy content in comparison to alternative prey, such as European Perch *Perca fluviatilis* (https://bit.ly/3yj08ER), which is the most abundant fish species in most freshwater lakes in Sweden (Wiklund & Ottosson 2020). Directing the foraging flights towards lakes with abundant stocks of fish with high energy content may help to make the provisioning of food to the chicks more energy-effective and to minimize the need of foraging trips (Rizzolo *et al.* 2015).

Having in mind the strong link between breeding site and foraging waters, it follows that the flight corridors should be kept free from barriers, such as wind turbines. For the guidance of such planning, it should be considered that the loons most often take the shortest route between the foraging water and the breeding pool, once they have gained height (Eriksson unpubl.), and that many pairs direct most (but far from all) foraging flights towards the same lake (Eriksson *et al.* 1990).

The benefit of open mire areas around the pools raises some concern in a long-term perspective. Results from The Swedish National Forest Inventory ('Riksskogstaxeringen') indicate a general tendency of tree overgrowth on mires over recent decades in large parts of Sweden. Most likely, this is a combined effect of changes in land-use, having in mind that open mires were used for grazing and hay-making historically, and that mires have been affected by drainage for forestry purposes in more recent decades. Other contributing factors include increased deposition of airborne nitrogen pollutants and climate impact (Gunnarsson *et al.* 2010).

ENVIRONMENTAL IMPACT ASSESSMENTS

Identification of breeding sites for Red-throated Loon is often a main issue in EIAs for various plan and projects. In general, the assessments are based on field surveys during just one or a few breeding seasons, with a risk that the dynamics in the choice of breeding sites may be overlooked as temporarily abandoned pools may not have been considered. Furthermore, complementary historical information about breeding sites used in the past is often fragmentary or missing. This has raised the question if field surveys with focus on some habitat characteristics that can be mapped during a single site visit can provide equally or more reliable results, and be more work-effective.

The current model alone is not suitable for accurate predictions of pool occupancy by Red-throated Loons. For instance, although predicted pool occupancy probability was significantly correlated with the proportion of years a pool was observed to be occupied, the prediction intervals (Figure 3, left) were very wide indicating that predicted values for a new pool can cover a wide range of values. Rather, assessments primarily based on habitat characteristics should be used only complimentary, e.g. within a 3-step approach that we propose for EIAs for plans and projects where breeding sites for Red-throated Loon may be affected:

1. Field surveys, not restricted to a single season and on a level that will provide reliable information to make it possible to assess the presence of a stationary pair and breeding success, e.g. an approach similar to the method used for assessing breeding success and the survival of pre-fledged chicks in this study.
2. Check of relevant databases, such as Artportalen, https://www.artportalen.se, for Sweden, historical data (if any) and contacts with persons having good knowledge about the local and regional bird fauna, in order to get complementary information for previous seasons as well as historical information about breeding pools used in past times.
3. Complementary assessments of potential breeding pools with no information about the presence of Red-throated Loon, now or in the past. Criteria for such complementary assessments shall include surface area of pools (primarily <1 ha), distance to potential foraging waters and extension of open mire area surrounding the pool. Ideally, the surveys should be done late enough during the season to allow accurate assessment of the coverage of floating vegetation.

It is equally important to include reliable assessments of the freshwaters used for foraging, and the flight routes between breeding pools and foraging waters, in addition to potential breeding pools. We recommend that this often-overlooked aspect should be covered by including all potential foraging waters up to a distance of approximately 9 km from each one of the pools with the confirmed presence of a stationary pair or assessed as potential breeding site, as follows:

- Information about the presence of foraging Red-throated Loon in these freshwaters. Information in relevant databases, such as Artportalen for Sweden, https://www.artportalen.se, and local knowledge might be guiding, but complementary field surveys are likely required, to be done during the period mid-June–mid-August, when pre-fledged chicks are fed by their parents.
- Also, information about the fish fauna in these freshwaters might be guiding, focusing on identifying waters with stocks of small-sized salmonid and cyprinid fish, primarily Vendace and Whitefish, <20 cm length. Information might be available via relevant databases, for Sweden the NORS database, https://www.slu.se/institutioner/akvatiska-resurser/

databaser/databas-for-sjoprovfiske-nors, and local knowledge.

- Identification of flight routes between breeding pools and freshwaters used for foraging, considering the shortest routes between the breeding pools and foraging waters and that many pairs direct most of the foraging flights towards the same lake (Eriksson *et al.* 1990). Taking those aspects into account, a reliable mapping of the flight routes might be possible on the basis of information about breeding pools and foraging waters, provided that it has been adequately collected. However, and whenever possible, the field surveys should also include pools with pairs feeding chicks, in order to identify the inflight and departure directions by the adult birds by direct observations. This might help to increase the accuracy of the mapping of flight routes.

Conclusion

On the basis of the outcome of this study we emphasize the importance of taking into account the surface area of breeding pools, their location in relation to foraging freshwaters and the extent of surrounding open mire as main habitat characteristics to be considered in nature conservation planning and management. Also, the importance of foraging waters must be addressed more adequately in future environmental impact assessments.

If the model on pool occupancy is to be improved to become more useful for future predictions of suitable pools from habitat characteristics, this might for example include refitting with data from more pools, and especially pools with a zero and low proportion of occupied years, as our dataset contained few of these pools. The inclusion of additional covariates might also be considered, to include *inter alia* reliable assessments of nest predation risk (as was done by Rizzolo *et al.* 2014) or fish data for freshwaters located within distances to be potentially used for foraging.

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Svensk sammanfattning

Smålommen är en förhållandevis sällsynt häckfågel i Sverige, med en population på 1 300–1 900 par. Liksom alla lommar livnär den sig nästan uteslutande på fisk, men i motsats till storlommen häckar den främst vid tjärnar och småvatten, ofta mindre än 1 ha. Det finns en långsiktig dynamik i valet av häckningstjärnar, med övergivna boplatser, återetableringar och nyetableringar. Bopredation bedöms vara en av drivkrafterna bakom denna dynamik.

Häckningstjärnarna är i regel fisktomma, och ungarna matas med fisk som föräldrarna hämtar från större klarvattenssjöar eller från havet upptill ett avstånd på 8–9 km, ibland längre. Därför måste förvaltningen ske i ett landskapsperspektiv som beaktar häckningsplatser såväl som fiskevatten och flygrutterna däremellan.

Smålommen har beaktats i fågelskyddsarbetet sedan lång tid. Arten är förtecknad i bilaga 1 till EU:s fågeldirektiv vilket innebär att 'särskilda åtgärder för bevarande av deras livsmiljö vidtas för att säkerställa deras överlevnad och fortplantning inom det område där de förekommer' (artikel 4.1 i direktivet). För svensk del finns indikationer på en långsiktig minskning, och åtskilliga tjärnar och småvatten med namn som 'Lomtjärnen' och liknande antyder att arten var vanligare och mera spridd i äldre tider. Data från Svensk Fågeltaxerings standardrutter pekar emellertid på en ökning i landets centrala och norra delar under de senaste årtiondena, i kontrast till de indikationer på ett försämrat häckningsutfall i stora delar av landet som erhållits genom de årliga uppföljningarna inom Projekt Lom.

Vi har undersökt nyttjandet av olika tjärnar och häckningsutfallet i relation till ett urval av habitatvariabler i ett barrskogsområde i mellersta Sverige, där smålommarna är hänvisade till födosök i större klarvattenssjöar. Vi har gjort undersökningen bland annat mot bakgrund av att lokaliseringen av häckningsplatser och fiskevatten är av central betydelse i miljökonsekvensbedömningar (MKB) för olika arbetsföretag där smålommen kan påverkas. Med hänsyn till den långsiktiga dynamiken i smålommens val av häckningstjärnar är det nödvändigt att även beakta tillfälligt övergivna häckningsplatser, utöver dem som kan lokaliseras under inventeringar under bara en eller ett fåtal häckningssäsonger. Detta har väckt frågor om det är möjligt att man genom att inventera ett antal habitatvariabler på ett trovärdigt sätt kan identifiera tänkbara häckningsvatten mera tidseffektivt.

UNDERSÖKNINGSOMRÅDE OCH METODIK

Undersökningen genomfördes inom ett 1 820 km^2 stort barrskogs- och myrområde i Malung-Sälens kommun i Dalarna (figur 1). Dalarna bildar tillsammans med omgivande län (Värmland, Örebro, Västmanland) kärnområdet för det svenska smålomsbeståndet, med totalt 470–600 par eller ungefär en tredjedel av populationen. Fisk till ungarna hämtas nästan uteslutande i näringsfattiga klarvattensjöar med god tillgång på småvuxen laxartad och mörtartad fisk. I undersökningsområdet finns ungefär 70 smålomspar, och populationen har varit föremål för årliga uppföljningar av häckningsutfallet sedan 1990-talet.

Habitatvariabler

För 41 häckningstjärnar inom undersökningsområdet (figur 1, fyllda cirklar) insamlades information om 23 variabler som redovisas i tabell 1 tillsammans med kortfattad information om metoden för datainsamling. Efter en gallring av samvarierande variabler återstod 16 som ingick i de statistiska analyserna (se även tabell 1):

- Areal: I tidigare undersökningar har man ibland funnit att små tjärnar (<1 ha) är de som är mest attraktiva för häckande smålommar och som har det bästa häckningsutfallet.
- Flikighetsindex (SLD), där SLD=1 avser en cirkelrund tjärn och högre värden indikerar en mångformighet vad gäller strandens flikighet och antal småöar. Ett högt SLD-värde kan antas indikera bättre förutsättningar för en god häckningsframgång.
- Antal småöar: Bon belägna på öar har i en del undersökningar visat sig vara mindre känsliga för predation och mänskliga störningar. Men resultaten är inte helt entydiga vilket torde bero på vilka predatorer som dominerar. Häckning på småöar torde vara en bra strategi för ett minska risken för predation från däggdjur, men inte lika effektiv mot predation från fåglar.
- Antal småöar belägna mer än 3 m från stranden, under antagandet att de torde vara mindre sårbara för predation från t.ex. rödräv.
- Genomströmmande vatten, under antagandet att tjärnar med genomströmmande vatten kanske är mindre sårbara för variationer i vattennivån och stigande vatten med risk för översvämmade bon efter perioder med mycket regn.
- Rensat utlopp, mot bakgrund av att man i tidigare undersökningar har funnit en koppling mellan att häckningstjärnar har övergivits och att utloppet har rensats eller dikats.
- Avstånd till närmast belägna sjö eller vattendrag som nyttjas för födosök, under antagandet att flygturerna mellan häckningstjärn och fiskevatten är energikrävande och att de därför riktas till närmast belägna sjö eller vattendrag med god tillgång på bytesfisk. Frågeställningen har undersökts i tidigare undersökningar, men resultaten är inte helt entydiga.
- Avstånd till väg, körbar för fyrhjulsdrivet fordon, som en indikator på hur utsatt tjärnen kan antas vara för mänskliga störningar.
- Täckning av halvgräs och sjöfräken inom en zon på 0–5 m från stranden.
- Täckning av vattenklöver inom en zon på 0–5 m från stranden.
- Täckning av vitmossa inom en zon på 0–5 m från stranden.
- Täckning av stående vegetation i vattnet, inom en zon på 0–5 m från strandkanten.
- Täckning av flytande vegetation i vattnet, inom en zon på 0–5 m från strandkanten.
- Avstånd till närmaste buskage.
- Avstånd till närmaste träd. Båda avståndsvariablerna tjänade som mått på bredden av ett öppet myrbälte kring tjärnen.
- Proportionen gungfly utefter strandlinjen, som ett mått på utbredningen av lämpliga stränder för placering av ett bo.

En sammanställning av medel- och medianvärden samt variationsbredd för habitatvariablerna återfinns i tabell 2 och primärdata i appendix 1a och 1b.

Nyttjande av häckningstjärnar och häckningsutfall

Undersökningen innefattade tre responsvariabler:

- Nyttjandet av häckningstjärnar: Kriteriet för att bedöma närvaron av ett potentiellt häckande par var att fåglar uppträdande i par har setts vid åtminstone två tillfällen med minst 15 dagars mellanrum, om inte häckning kunde fastställas genom fynd av ägg, observation av ruvande fågel eller icke flygga ungar.

Närvaron av ett potentiellt häckande par, eller *stationärt par*, bedömdes årligen för varje tjärn med tillräcklig information för en sådan bedömning.

- Häckningsframgång: För varje stationärt par och för varje år undersöktes häckningsframgången genom närvaro eller frånvaro av åtminstone en *stor unge*, som uppnått minst halva längden i relation till föräldrafåglarna. I regel behövdes det 2–4 besök till varje tjärn för att få tillräcklig information. Det första besöket gjordes före eller under ruvningsperioden, för att minska risken att misslyckade häckningsförsök undgick att bli upptäckta. Tidpunkten för det sista besöket anpassades till ungens/ungarnas tillväxt tills de blivit mer än halvstora, eller att frånvaro av unge/ungar kunde fastställas.
- Antal stora ungar, som ett mått på ungarnas överlevnad. Lommarna lägger i regel två ägg, och ungarnas överlevnad är till stor del beroende på hur framgångsrika föräldrarna är i sina matningsbestyr. Dessa bedömningar innefattade häckningar som upptäcktes först efter att ungarna hade kläckts.

Alla de 41 tjärnarna ingick i analyserna avseende nyttjandet av tjärnar och häckningsframgången, medan det fanns underlag från 39 tjärnar för analyserna av ungarnas överlevnad.

Statistiska analyser

För var och en av de tre responsvariablerna undersöktes eventuella samband med de olika habitatvariablerna med generaliserade linjära modeller. Antalet habitatvariabler begränsades till fyra, med hänsyn till att 39–41 tjärnar ingick i modellerna, och urvalet gjordes med ledning av tidigare kunskap om vilka som kunde antas vara de mest relevanta. Utfallet värderades med hjälp av AIC (Akaikes informationskriterium) för alternativa kandidatmodeller, med en variabelvikt ≥0.4 som gränsvärde för bedömningen om en viss habitatvariabel stödde modellen. Genom korsvalidering undersöktes möjligheten att utvärdera lämpligheten av olika tjärnar och småvatten enbart med ledning av ett urval av habitategenskaper.

För att täcka upp för risken att vi missat någon viktig habitatvariabel i det initiala urvalet utvärderades modellerna genom att undersöka om utfallet förbättrades genom att inkludera fler habitatvariabler, genom en s.k. “Random Forest-algoritm”.

RESULTAT

I genomsnitt per år var 79% av de 41 tjärnar som ingick undersökningen bebodda av smålom, och vi noterade aldrig mer än ett stationärt par i varje tjärn (primärdata i appendix 2). Häckningsutfallet var i medeltal 0,66 stora ungar per stationärt par och år, och den genomsnittliga andelen ungkullar med två stora ungar var 28% per år (primärdata i appendix 3 och 4). Häckningsutfallet låg alltså på samma nivå som för Svealand (med Dalsland) i stort under perioden 1994–2018.

Modellerna indikerade att förhållandevis små tjärnar med utbredd flytande vegetation var de mest attraktiva för häckande smålommar, men att kort avstånd till närmaste fiskevatten och till omgivande träd hade svagare betydelse för val av häckningstjärn (figur 2, tabell 3). Ungarnas överlevnad var bättre i tjärnar belägna nära fiskevatten och med större utbredning av ett öppet myrbälte kring tjärnen (figur 4, tabell 3). Vidare fanns det ett svagt stöd för bedömningen att häckningsframgången var bättre i små tjärnar med öppen terräng kring tjärnen (tabell 3). Precisionen i modellernas utfall var emellertid inte tillräcklig för bedömningar av olika tjärnars lämplighet, enbart med ledning av ett antal habitategenskaper (figur 3). För detaljer angående utfallet av de statistiska analyserna hänvisas till den engelska texten.

Vad gäller smålommens nyttjande av olika tjärnar var variationen mellan tjärnar större än variationen mellan olika år, medan det motsatta förhållandet gällde för ungarnas överlevnad. För häckningsframgången var variationen mellan år nära noll, medan variationen mellan tjärnar var större.

“Random Forest-modellerna”, innefattande alla de 16 habitatvariablerna, visade inte på någon ökad förklaringsgrad.

DISKUSSION

För smålommen i det nordiska barrskogslandskapet, och där lommarna är hänvisade till födosök i större klarvattenssjöar, gäller med en viss grad av generalisering att den idealiska smålomstjärnen är mindre än 1 ha, ligger förhållandevis nära lämpliga fiskevatten och omges av ett öppet myrbälte i barrskog. Det faktum att modellen för häckningsutfall bara gav ett svagt utfall, och enbart med avseende på tjärnens areal och avstånd till buskage, torde bero på ett generellt högt predationstryck som inte kunde vägas in i analyserna.

Lokaliseringen av häckningsplatserna är en viktig aspekt att beakta i miljökonsekvensbeskrivningar (MKB) för olika arbetsföretag där smålommen kan påverkas. Ofta bygger bedömningar på fältarbete under bara ett eller ett fåtal år. Då kan dynamiken i smålommens val av häckningsplatser inte fångas upp, och det finns risk att man missar häckningsplatser som tillfällig har stått tomma under något eller några år. Dessutom saknas ofta informationen från tidigare år, eller den är fragmentarisk. Detta har väckt frågan om det är möjligt att i stället fokusera fältarbetet på ett antal egenskaper som karteras vid ett enda tillfälle och att den informationen kan tjäna som underlag för en bedömning om tjärnens lämplighet för häckande smålommar. Träffbilden för en bedömning av en enskild tjärn med ledning av ett antal habitategenskaper var emellertid låg, med avseende både på hur ofta en tjärn kunde antas vara bebodd av ett smålomspar och förutsättningarna för ungarnas överlevnad (figur 3). Vi rekommenderar att bedömningar baserade på habitatkaraktärer bara ska användas som ett komplement, t. ex. inom ramen för en trestegsansats:

1. Fältundersökningar som inte begränsas till en enda häckningssäsong, med syftet att ge underlag för trovärdiga bedömningar om närvaron av stationära par och häckningsutfallet.
2. Genomgång av relevanta databaser, såsom Artportalen, https://www.artportalen.se/, eftersök av historisk information och kontakter med personer med god kännedom om det lokala fågellivet, för få kompletterande information.
3. Kompletterande bedömningar i fält av tänkbara häckningstjärnar utan information om smålommar, med fokus små tjärnar (främst <1 ha), avstånd till tänkbara fiskevatten och utbredning av öppen myrmark kring tjärnen. Helst bör fältarbetet göras tillräckligt sent under säsongen så att man även kan kartera förekomsten av flytande vegetation.

Men det är lika viktigt att beakta tänkbara fiskevatten och flygvägarna mellan häckningstjärnar och fiskevatten, en ofta förbisedd aspekt. MKB:n bör innefatta en bedömning av alla tänkbara fiskevatten upp till avstånd av ungefär 9 km från varje tjärn med fastställd närvaro av stationärt par eller som har bedömts vara en lämplig häckningsplats, förslagsvis enligt följande:

- Information om förekomsten av fiskande smålom i dessa sjöar. Uppgifter i Artportalen och från personer med lokalkännedom kan vara vägledande, men oftast torde kompletterande fältstudier behövas, lämpligen under den period då smålommen matar sina ungar, dvs. mellan början-mitten av juli och mitten av augusti.
- Även information om fiskfaunan i de olika sjöarna kan ge vägledning, med fokus på sjöar med goda bestånd av småvuxen (<20 cm) laxartad och mörtartad fisk, primärt sik och siklöja. Information kan finnas i relevanta databaser, såsom Nationellt register över sjöprovfisken (NORS, https://www.slu.se/institutioner/akvatiska-resurser/databaser/databas-for-sjoprovfiske-nors/) eller erhållas genom lokal kännedom.
- Kartering av flygvägarna mellan häckningstjärnar och fiskevatten, med beaktande av att smålommarna ofta (men inte alltid) företar sina födosöksturer till samma eller ett fåtal sjöar. Närhelst det är möjligt bör fältarbetet innefatta observationspass vid häckningstjärnar med ungar, för att identifiera de adulta fåglarnas in- och utflygningsriktningar genom direktobservationer.

Vår undersökning pekar på att förvaltningen av smålommen måste ske i ett landskapsperspektiv som utöver häckningsplatserna också beaktar fiskevattnen, och flygvägarna mellan dessa.

Appendices

APPENDIX 1A. Primary data for habitat characteristics.
— Primärdata för habitategenskaper.

					Number of islets *Antal småöar*							
Pool number *Tjärn nummer*	Surface area (km^2) *Areal (km^2)*	Shore length (km) *Strandlängd (km)*	Shoreline development index (SLD) *Flikighets-index (SLD)*	Maximum distance over open water (m) *Största avstånd över öppet vatten (m)*	Total *Totalt*	Judged to be appropriate for nesting *Bedömts lämpliga för häckning*	Total, >3 m from the shore *Totalt, >3 m från stranden*	Judged to be appropriate for nesting, >3 m from the shore *Bedömts lämpliga för häckning, >3 m från stranden*	Water throughflow *Genom-strömmande vatten*	Cleared outlet *Rensat utlopp*	Distance to the nearest foraging freshwater (km) *Avstånd till fiskevatten (km)*	Distance to road (km) *Avstånd till väg (km)*
21	0.003	0.21	1.1	110	24	17	1	1	1	0	1.9	0.4
23	0.013	0.79	2.0	200	11	9	0	0	0	0	1.1	0.1
24	0.007	0.71	2.4	220	14	10	1	1	0	0	0.7	0.3
25	0.007	0.52	1.8	140	28	15	5	5	0	0	0.4	0.6
31	0.002	0.21	1.3	60	16	11	0	0	0	0	0.7	0.2
32	0.004	0.65	2.9	90	13	10	1	1	1	0	0.5	0.1
43	0.006	0.35	1.3	120	5	3	3	2	0	0	0.9	0.8
44	0.005	0.33	1.3	100	8	4	4	2	0	0	0.2	0.9
49	0.009	0.57	1.7	150	31	27	1	1	1	0	1.5	0.4
51	0.003	0.60	3.1	170	9	9	1	1	0	0	0.4	0.2
52	0.004	0.45	2.0	130	6	5	1	1	0	0	0.2	0.1
53	0.009	0.80	2.4	320	1	0	0	0	1	1	0.2	0.1
54	0.009	0.46	1.4	170	4	2	0	0	0	0	1.0	0.1
55	0.007	0.47	1.6	150	22	22	3	3	1	0	1.4	0.2
57	0.035	0.86	1.3	270	26	26	4	4	0	0	1.0	0.6
58	0.041	0.80	1.1	250	51	50	0	0	0	0	0.5	0.1

APPENDIX 1A continued *fortsatt.*

						Number of islets *Antal småöar*						
Pool number *Tjärn nummer*	Surface area (km^2) *Areal (km^2)*	Shore length (km) *Strandlängd (km)*	Shoreline development index (SLD) *Flikighets-index (SLD)*	Maximum distance over open water (m) *Största avstånd över öppet vatten (m)*	Total *Totalt*	Judged to be appropriate for nesting *Bedömts lämpliga för häckning*	Total, >3 m from the shore *Totalt, >3 m från stranden*	Judged to be appropriate for nesting, >3 m from the shore *Bedömts lämpliga för häckning, >3 m från stranden*	Water throughflow *Genom-strömmande vatten*	Cleared outlet *Rensat utlopp*	Distance to the nearest foraging freshwater (km) *Avstånd till fiskevatten (km)*	Distance to road (km) *Avstånd till väg (km)*
61	0.005	0.28	1.1	90	37	30	0	0	0	0	0.2	0.3
63	0.007	0.50	1.7	160	4	4	0	0	0	0	2.2	0.1
65	0.029	1.64	2.7	330	37	21	2	2	1	0	1.4	0.3
66	0.004	0.30	1.3	90	6	5	1	0	0	0	0.5	0.2
68	0.004	0.47	2.1	110	12	12	0	0	0	0	0.6	0.4
69	0.003	0.28	1.4	80	3	3	0	0	0	0	0.0	0.8
70	0.014	0.94	2.2	200	19	19	0	0	0	0	1.0	0.8
74	0.004	0.25	1.1	90	19	18	5	5	0	0	0.1	0.1
80	0.002	0.20	1.3	80	14	12	3	3	0	0	0.3	0.3
81	0.003	0.64	3.3	120	13	10	2	2	0	0	0.2	0.3
82	0.001	0.25	2.3	90	10	7	3	3	0	0	0.1	0.3
91	0.014	0.72	1.7	320	2	2	1	1	1	1	0.3	0.1
92	0.014	0.68	1.6	160	14	14	9	9	0	0	1.2	0.1
93	0.003	0.31	1.6	80	58	58	12	12	0	0	3.5	0.4
95	0.013	0.54	1.3	160	2	2	0	0	0	0	4.9	0.2
96	0.005	0.41	1.6	130	12	10	0	0	0	0	2.5	0.1
97	0.013	0.66	1.6	190	26	25	1	1	0	0	2.2	0.2
99	0.006	0.47	1.7	100	3	2	0	0	0	0	0.1	0.3
100	0.030	0.80	1.3	220	10	7	1	1	0	0	1.0	0.1

APPENDIX 1A continued *fortsatt.*

						Number of islets *Antal småöar*						
Pool number *Tjärn nummer*	Surface area (km^2) *Areal (km^2)*	Shore length (km) *Strandlängd (km)*	Shoreline development index (SLD) *Flikighets-index (SLD)*	Maximum distance over open water (m) *Största avstånd över öppet vatten (m)*	Total *Totalt*	Judged to be appropriate for nesting *Bedömts lämpliga för häckning*	Total, >3 m from the shore *Totalt, >3 m från stranden*	Judged to be appropriate for nesting, >3 m from the shore *Bedömts lämpliga för häckning, >3 m från stranden*	Water throughflow *Genom-strömmande vatten*	Cleared outlet *Rensat utlopp*	Distance to the nearest foraging freshwater (km) *Avstånd till fiskevatten (km)*	Distance to road (km) *Avstånd till väg (km)*
101	0.007	0.42	1.4	140	8	6	2	1	1	0	1.5	0.2
102	0.023	1.06	2.0	300	1	1	1	1	0	0	1.8	0.0
103	0.010	0.62	1.7	210	7	6	3	3	1	0	2.3	0.8
107	0.004	0.29	1.3	100	5	5	1	1	0	0	1.5	0.2
111	0.013	0.63	1.6	200	14	14	5	5	1	0	3.5	0.4
113	0.014	0.47	1.1	180	15	15	0	0	0	0	3.5	0.3

Note: Pool numbers are the same is in Appendix 4 in Dahlén & Eriksson (2002), except for pool number 113 that was included in the surveys only after the period covered in that paper. Single discrepancies in relation to the previous publication depend on updated or revised information.

Observera: Numreringen av tjärnar är densamma som i appendix 4 i Dahlén & Eriksson (2002), förutom för tjärn nummer 113 som kom med i undersökningen först senare. Enstaka avvikelser i jämförelse med den tidigare publikationen beror på uppdaterad eller reviderad information.

APPENDIX 1B. Primary data for habitat characteristics.
– Primärdata för habitategenskaper.

	Coverage (%) of shoreline vegetation around the pool *Täckning (%) av strandkantsvegetation*					Coverage (%) of vegetation in the water *Vegetationstäckning (%) i vattnet*			Width of open mire belt (m) *Bredd av öppet myrbälte (m)*		
Pool number *Tjärn nummer*	Cyperaceae and *Equisetum fluviatile* *Halvgräs och sjöfräken*	*Menyanthes trifoliata* *Vattenklöver*	Total *Totalt*	*Sphagnum* mosses *Vitmossor*	Height of vegetation (cm) *Vegetationshöjd (cm)*	Standing/ emergent vegetation *Stående vegetation*	Floating vegetation *Flytande vegetation*	Standing/emergent + floating vegetation *Stående + flytande vegetation*	From shoreline to closest scrub *Från stranden till närmaste buske*	From shoreline to closest tree *Från stranden till närmaste träd*	Quagmire along the shore (%) *Gungfly utefter stranden (%)*
21	19	18	37	5	28	7	10	17	48	48	100
23	6	5	11	4	13	5	20	25	23	27	95
24	1	1	2	2	11	2	5	7	77	85	100
25	6	0	7	24	10	5	80	80	7	150	50
31	1	0	1	3	4	4	0	4	23	155	95
32	10	0	10	10	13	5	2	7	31	35	100
43	5	3	8	16	21	5	25	25	15	27	90
44	5	3	8	4	9	5	5	10	29	216	90
49	9	4	13	3	7	1	2	3	53	36	100
51	21	2	23	22	14	5	7	7	255	334	100
52	29	11	41	8	31	5	20	25	21	103	100
53	4	1	5	12	5	5	5	5	44	49	100
54	5	1	6	3	11	5	0	5	37	69	100
55	4	0	4	1	4	5	5	5	26	83	100
57	5	0	5	2	3	5	5	5	35	49	100
58	4	0	5	6	12	5	5	5	11	24	100
61	3	0	5	2	7	5	20	20	74	169	100
63	4	0	4	7	9	5	5	5	27	63	95

APPENDIX 1B continued *fortsatt.*

	Coverage (%) of shoreline vegetation around the pool *Täckning (%) av strandkantsvegetation*					Coverage (%) of vegetation in the water *Vegetationstäckning (%) i vattnet*			Width of open mire belt (m) *Bredd av öppet myrbälte (m)*		
Pool number *Tjärn nummer*	Cyperaceae and *Equisetum fluviatile* *Halvgräs och sjöfräken*	*Menyanthes trifoliata* *Vattenklöver*	Total *Totalt*	*Sphagnum* mosses *Vitmossor*	Height of vegetation (cm) *Vegetationshöjd (cm)*	Standing/ emergent vegetation *Stående vegetation*	Floating vegetation *Flytande vegetation*	Standing/emergent + floating vegetation *Stående + flytande vegetation*	From shoreline to closest scrub *Från stranden till närmaste buske*	From shoreline to closest tree *Från stranden till närmaste träd*	Quagmire along the shore (%) *Gungfly utefter stranden (%)*
65	2	0	3	1	8	5	5	5	31	42	100
66	14	0	15	17	12	5	5	5	47	142	100
68	24	0	24	10	18	5	4	4	26	26	100
69	10	2	12	4	10	5	5	5	195	202	100
70	12	0	12	7	10	5	5	5	37	40	100
74	0	0	3	12	3	5	0	5	12	259	10
80	2	0	2	1	4	0	0	0	91	95	60
81	4	0	5	0	6	0	0	0	43	164	30
82	4	0	13	12	14	0	0	1	6	127	30
91	15	1	16	4	17	5	5	5	13	26	100
92	31	18	57	21	40	20	45	65	80	88	100
93	2	0	2	5	3	0	0	0	74	76	80
95	38	5	43	30	37	5	5	5	67	72	100
96	1	0	1	0	1	5	30	30	29	33	90
97	6	1	9	1	9	10	30	40	47	49	98
99	3	0	5	1	7	5	5	5	46	139	35
100	2	0	2	14	7	0	5	5	60	63	75
101	8	1	9	7	21	5	10	10	34	42	90
102	13	6	20	13	19	5	5	5	55	72	100

APPENDIX 1B continued *fortsatt*.

	Coverage (%) of shoreline vegetation around the pool *Täckning (%) av strandkantsvegetation*					Coverage (%) of vegetation in the water *Vegetationstäckning (%) i vattnet*			Width of open mire belt (m) *Bredd av öppet myrbälte (m)*		
Pool number *Tjärn nummer*	Cyperaceae and *Equisetum fluviatile* *Halvgräs och sjöfräken*	*Menyanthes trifoliata* *Vattenklöver*	Total *Totalt*	*Sphagnum* mosses *Vitmossor*	Height of vegetation (cm) *Vegetationshöjd (cm)*	Standing/ emergent vegetation *Stående vegetation*	Floating vegetation *Flytande vegetation*	Standing/emergent + floating vegetation *Stående + flytande vegetation*	From shoreline to closest scrub *Från stranden till närmaste buske*	From shoreline to closest tree *Från stranden till närmaste träd*	Quagmire along the shore (%) *Gungfly utefter stranden (%)*
103	16	0	24	9	16	5	40	40	22	32	70
107	40	0	40	27	21	20	25	45	28	33	100
111	8	7	15	6	20	5	5	5	96	102	100
113	5	2	8	0	10	5	5	5	37	41	100

Note: Pool numbers are the same is in Appendix 4 in Dahlén & Eriksson (2002), except for pool number 113 that was included in the surveys only after the period covered in that paper. Single discrepancies in relation to the previous publication depend on updated or revised information. Standing/emergent and floating vegetation overlapped in some pools, why the total can be smaller than the individual estimates for each habitat characteristic.

Observera: Numreringen av tjärnar är densamma som i appendix 4 i Dahlén & Eriksson (2002), förutom för tjärn nummer 113 som kom med i undersökningen först senare. Enstaka avvikelser i jämförelse med den tidigare publikationen beror på uppdaterad eller reviderad information. Stående och flytande vegetation överlappade, varför totalen kan bli mindre än de enskilda skattningarna för varje habitategenskap.

APPENDIX 2. Primary data for pool occupancy. 1=Occupied by one stationary pair, 0=Not occupied.
— Primärdata för nyttjande av tjärnar. 1=Nyttjad av ett stationärt par, 0=Ej nyttjad.

Pool number *Tjärn nummer*	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	% years with pair *% år med par*	Number of years *Antal år*
21	1	1	1	1	1	1	1	1	1	1																	100	10
23	1	1	1	1	1	0	1	1	1		1	1	1														92	12
24	1	1	1	1	1	1	1	1	1			1															100	10
25	1	0	1	1	1	1	1	1	1	1	1		1		1												92	13
31	1	1	1	1	1	1																					100	6
32	1	1	1	1	1	1		0																			86	7
43	1	1	1	1	1	1					1	1															100	8
44	1	1	1	1	1	0							1														86	7
49				1	1	1			1	1		1	1	1	1	1	0										91	11
51	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	85	26
52	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	96	26
53	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	0	1	1	0	1	0	1	0	0	0	65	26
54				1	1	1	1	0		0	0				1	0	1	0	0		0	0	0	0	0	0	33	18
55	1	1	1	1	1	1	1	1	0	1	0	1			0	1	1	0	0	1	0	0	0	0	1	1	63	24
57	1	1	1	1	1	1	1	1	1	1	1	0		0	0	1	1	0		1	0		0	0	0	0	61	23
58	1		1	1	1	1	1	0	1							1	0		0					0	0		62	13
61	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0		1								89	18
63		1								0							0	0		0		1	1	0	0	1	40	10
65	1	1	1	1	1	1	1	1	0		1		0														82	11
66	1	1	1		1	1	1	0	1	0	0						0		1		0			0	0		47	15
68		1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1		1	1	1	0	0		91	22
69				1			1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	95	21

APPENDIX 2 continued *fortsatt.*

Pool number *Tjärn nummer*	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	% years with pair *% år med par*	Number of years *Antal år*
70					1	1	1	1	1	1				0			0	0	1		0	1	1	0	1	1	69	16
74	1		1	1	1	1	1	1	1	1		1	1	1	0	1				1							93	15
80	1	1	1	1	1	1		0	1		0	1	1														82	11
81	1	1	1	1	1	1		0	0		0																67	9
82	1	1	1	1	1	1	1	0	0		1																80	10
91	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	96	26
92	1	1	1	1	1	1	1		1	1	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1	1	84	25
93	1	1	1	1	1	1		1	1	0	1				1	1	1	1		1	1	1	1	0	1		90	20
95				1	1	1	1	1	0	1	1	0	0		0	0	0		0	0		0	1		0	0	42	19
96	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	92	26
97	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	96	26
99	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	96	26
100	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	85	26
101	1	1	1	1	1	1	1	1	1		0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	92	25
102	1	1	1					0	1	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	21
103				0	1	1	1	1	1	1	1	1	1	1	1	1	0	0		1	0		0		1		74	19
107				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	100	23
111						1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	0	0	1	1	90	20
113								1	0	0		1	1	1	0	0	1	1			0	0	0		1	1	53	15

Note: Pool numbers are the same is in Appendix 4 in Dahlén & Eriksson (2002), except for pool number 113 that was included in the surveys only after the period covered in that paper.
Observera: Numreringen av tjärnar är densamma som i appendix 4 i Dahlén & Eriksson (2002), förutom för tjärn nummer 113 som kom med i undersökningen först senare.

APPENDIX 3. Primary data for breeding success.
— Primärdata för häckningsutfall.

	Number of chicks *Antal ungar*																											
Pool number *Tjärn nummer*	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	Mean per year *Medel-värde per år*	Number of years *Antal år*
21	2	1	1	2	1	0	0	1	2	1																	1.10	10
23	0	1	1	1	0		1	1	1		0	0															0.60	10
24	2	1	1	1	0	1	0	1	1																		0.89	9
25	0		0	0	0	1	0	0	0				1		0												0.20	10
31	2	0	0	0	0	0																					0.33	6
32	2	0	2	1	2	0																					1.17	6
43	0	0	0	0	0	1					1																0.29	7
44	0	0	0	0	0								0														0.00	6
49				1	1	1			1				2	2	2												1.43	7
51	2	2	0	0	1	2	1	1			2		0	0	0	0	0		1	0	1	1	1	1	1	2	0.86	22
52	0	0	0	0	2	1	0	1	1	2	2	1	0	0	0	0	0	0	0	0	0	0	0	1	1		0.48	25
53	0	2	0	0	0	0	0	0	1		0		0	0		1		0	0		0		1				0.29	17
54				0	1	0	0								0		0										0.17	6
55	0	1	1	0	0	0	0	0		1		0				0	0			0					2	1	0.40	15
57	2	0	2	0	0	2	1	1	1	2	1					0	0			0							0.86	14
58	0		0	0	0	0	1		0							0											0.13	8
61	1	0	1	1	2	2	1	0	1		0	0	2	2	2												1.07	14
63		2																				1	1			1	1.25	4
65	2	0	1	0	1	1		0			0																0.63	8
66	1	1	1		1	1	0		0										0								0.63	8
68		1	0	2	0	2	2	1	1	2	2	1	1	2		1	0	2	1		2	2	1				1.30	20

APPENDIX 3 continued *fortsatt.*

	Number of chicks *Antal ungar*																											
Pool number *Tjärn nummer*	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	Mean per year *Medel-värde per år*	Number of years *Antal år*
69							1	2	1	1		2	2		2	2	1	0	1	2	1	2	0		1	2	1.35	17
70					1	0	1	0	0	1	0												0		1	1	0.50	10
74	0		2	2	1	1	0	1	0	1		0		1		0				1							0.77	13
80	2	0	0		0	0			0				1														0.43	7
81	0	0	1	0	0	0																					0.17	6
82	2	1	1	1	0	0	0				1																0.75	8
91	0	1	0	0	1	0	0		1	1	1	2	2	1	0	0	0	1	1	0	0	0	0	0	1	1	0.56	25
92	1	0	1	0	2	0	0		0	0			2	2		2	0	0	2			1	0	2	0	0	0.75	20
93	1	1	0	1	0	1		1	0		0				0		0	0		1	0	1	2		0		0.53	17
95				0	0	0	0	0		0	0												0				0.00	8
96	0	1	0	0	1	1	0	0			0	1	0		1	2	1	0	1	0	1	0	1	0	0	0	0.48	23
97	0	1	0	0	2	1	0	1			1	1	1	2	1	2	2	0	0		1	0	1	0	1	1	0.83	23
99	2	1	1	1	2	1	1	1	0	0	0	2	0	2	0	0	1	0	2	2	0	1	0		0	0	0.80	25
100	1	0	0	1	2	2	1	1	0	1	1	0			0		1	0	0	0	1	0	0	0			0.57	21
101	0	0	0	0	1	1	0	1	1			1	1	0	1	1	1		1	1	1	1	0	0	2	0	0.65	23
102	1	0	0						1																		0.50	4
103					2	1	0	0	1	1	1	1	0		0	1				0					0		0.62	13
107				0	1	1	1	1	1	2	1	0	1	1	2	1	1	0	1	1	0	0	0	0	1	1	0.78	23
111						0		0	0	0	1	0	0	0	0	0	0		1		0	0			0	0	0.13	16
113								1				1	1	0			1								1	0	0.71	7

Note: Pool numbers are the same is in Appendix 4 in Dahlén & Eriksson (2002), except for pool number 113 that was included in the surveys only after the period covered in that paper.
Observera: Numreringen av tjärnar är densamma som i appendix 4 i Dahlén & Eriksson (2002), förutom för tjärn nummer 113 som kom med i undersökningen först senare.

APPENDIX 4. Primary data for successful pairs producing chicks.
— Primärdata för framgånsrika par med ungar.

	Number of chicks *Antal ungar*																											
Pool number *Tjärn nummer*	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	Mean per year *Medel-värde per år*	Number of years *Antal år*
21	2	1	1	2	1			1	2	1																	1.38	8
23		1	1	1			1	1	1				1														1.00	7
24.	2	1	1	1		1		1	1			1															1.13	8
25						1				1	1		1														1.00	4
31	2																										2.00	1
32	2		2	1	2																						1.75	4
43						1					1	1															1.00	3
44																											–	0
49				1	1	1			1	1		1	2	2	2	2											1.40	10
51	2	2			1	2	1	1			2								1		1	1	1	1	1	2	1.36	14
52					2	1		1	1	2	2	1												1	1		1.33	9
53		2							1							1							1				1.25	4
54					1																						1.00	1
55		1	1							1															2	1	1.20	5
57	2		2			2	1	1	1	2	1																1.50	8
58							1																				1.00	1
61	1		1	1	2	2	1		1	2			2	2	2												1.55	11
63		2																				1	1			1	1.25	4
65	2		1		1	1	1																				1.20	5
66	1	1	1		1	1																					1.00	5

APPENDIX 4 continued *fortsatt.*

	Number of chicks *Antal ungar*																											
Pool number *Tjärn nummer*	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	Mean per year *Medel-värde per år*	Number of years *Antal år*
68		1		2		2	2	1	1	2	2	1	1	2		1		2	1		2	2	1				1.53	17
69				2			1	2	1	1	2	2	2		2	2	1		1	2	1	2		1	1	2	1.56	18
70					1		1			1												2			1	1	1.17	6
74			2	2	1	1		1		1			1	1						1							1.22	9
80	2			1								1	1														1.25	4
81			1																								1.00	1
82	2	1	1	1							1																1.20	5
91		1			1				1	1	1	2	2	1				1	1						1	1	1.17	12
92	1		1		2								2	2	2	2			2			1		2			1.70	10
93	1	1		1		1		1								1				1		1	2				1.11	9
95																											–	0
96		1			1	1						1			1	2	1		1		1		1				1.10	10
97		1			2	1		1		1	1	1	1	2	1	2	2				1		1		1	1	1.25	16
99	2	1	1	1	2	1	1	1				2		2			1		2	2		1					1.43	14
100	1			1	2	2	1	1		1	1						1				1						1.20	10
101					1	1		1	1			1	1		1	1	1		1	1	1	1			2		1.07	14
102	1								1																		1.00	2
103					2	1			1	1	1	1				1											1.14	7
107					1	1	1	1	1	2	1		1	1	2	1	1		1	1					1	1	1.13	16
111							1				1							1	1								1.00	4
113								1				1	1				1	1							1		1.00	6

Note: Pool numbers are the same is in Appendix 4 in Dahlén & Eriksson (2002), except for pool number 113 that was included in the surveys only after the period covered in that paper. *Observera: Numreringen av tjärnar är densamma som i appendix 4 i Dahlén & Eriksson (2002), förutom för tjärn nummer 113 som kom med i undersökningen först senare.*

APPENDIX 5. Model selection results for pool occupancy: Regression coefficients, degrees of freedom (df), log-likelihood, AICc, ΔAICc and Akaike weights for models with a cumulative Akaike weight ≤ 0.95. The covariates pool area, distance to fishing pool and distance to nearest tree were log-transformed and all covariates were standardized before model fitting. Models with ΔAICc <2 are considered models with strong support (Burnham & Anderson 2004) and this threshold is indicated by a horizontal line.

— Resultat för val av modell för nyttjande av tjärnar: Regressionskoefficienter, frihetsgrader (df), logaritmered sannolikhet, AICc, ΔAICc och Akaike-vikter för modeller med en Akaike-vikt ≤0.95. Variablerna areal, avstånd till fiskevatten och avstånd till närmaste träd var log-transformerade och alla variablerna standardiserades inför modellanpassningen. Modeller med ΔAICc <2 bedöms vara modeller med starkt stöd (Burnham & Andersson 2004) och denna tröskel markeras med en horisontell linje.

Intercept	Floating vegetation (%) *Flytande vegetation (%)*	Lake area (km^2) *Areal (km^2)*	Distance to foraging lake (km) *Avstånd till fiskevatten (km)*	Distance to nearest tree (m) *Avstånd till närmaste träd (m)*	Year *År*	df	Log-likelihood *Logaritmerad sannolikhet*	AICc	ΔAICc	Akaike weight *Akaike-vikt*	Cumulative Akaike weight *Kumulerad Akaike-vikt*
2.025	0.524	−0.415			−1.172	6	−277.966	568.050	0.000	0.156	0.156
2.030	0.539	−0.486	−0.414	−0.476	−1.157	8	−276.049	568.302	0.252	0.137	0.293
2.028	0.501	−0.572		−0.335	−1.172	7	−277.179	568.516	0.466	0.123	0.416
2.041	0.547		−0.389		−1.184	6	−278.462	569.042	0.992	0.095	0.511
2.027	0.555	−0.325	−0.247		−1.162	7	−277.529	569.217	1.167	0.087	0.597
2.046	0.487				−1.208	5	−279.645	569.375	1.326	0.080	0.677
2.046	0.535		−0.530	−0.282	−1.188	7	−277.901	569.960	1.910	0.060	0.737
1.995		−0.381			−1.178	5	−280.165	570.414	2.364	0.048	0.785
1.999		−0.554		−0.366	−1.178	6	−279.310	570.738	2.689	0.041	0.826
2.017					−1.208	4	−281.431	570.919	2.869	0.037	0.863
1.999		−0.482	−0.348	−0.490	−1.167	7	−278.607	571.371	3.322	0.030	0.892
2.047	0.482			−0.045	−1.210	6	−279.628	571.375	3.326	0.029	0.922
2.010			−0.309		−1.191	5	−280.751	571.586	3.536	0.027	0.948

APPENDIX 6. Model selection for breeding success: Regression coefficients, degrees of freedom (df), log-likelihood, AICc, ΔAICc and Akaike weights for models with a cumulative Akaike weight ≤0.95. The covariates were standardized before model fitting. Models with ΔAICc <2 are considered models with strong support (Burnham & Anderson 2004) and this threshold is indicated by a horizontal line.
— Val av modell för häckningsutfall: Regressionskoefficienter, frihetsgrader (df), logaritmered sannolikhet, AICc, ΔAICc och Akaike-vikter för modeller med en Akaike-vikt ≤0.95. Variablerna standardiserades inför modellanpassningen. Modeller med ΔAICc <2 bedöms vara modeller med starkt stöd (Burnham & Andersson 2004) och denna tröskel markeras med en horisontell linje.

Intercept	Lake area (km^2) *Areal (km^2)*	Cleared outlet *Rensat utlopp*	Distance to foraging lake (km) *Avstånd till fiskevatten (km)*	Distance to scrub (m) *Avstånd till buske (m)*	df	Log-likelihood *Logaritmerad sannolikhet*	AICc	ΔAICc	Akaike weight *Akaike-vikt*	Cumulative Akaike weight *Kumulerad Akaike-vikt*
0.013					3	−362.267	730.579	0.000	0.134	0.134
0.029				0.236	4	−361.407	730.889	0.310	0.115	0.249
0.019	−0.193				4	−361.514	731.104	0.524	0.103	0.353
0.054		−0.662			4	−361.814	731.703	1.124	0.077	0.429
0.032	−0.164			0.205	5	−360.851	731.814	1.235	0.072	0.502
0.015			−0.135		4	−361.925	731.925	1.346	0.069	0.570
0.062		−0.560		0.217	5	−361.067	732.246	1.667	0.058	0.629
0.031			−0.131	0.232	5	−361.069	732.249	1.670	0.058	0.687
0.058	−0.185	−0.620			5	−361.095	732.303	1.723	0.057	0.744
0.067		−0.821	−0.177		5	−361.227	732.565	1.986	0.050	0.793
0.021	−0.179		−0.113		5	−361.267	732.646	2.067	0.048	0.841
0.075		−0.715	−0.168	0.206	6	−360.515	733.187	2.608	0.036	0.878
0.064	−0.159	−0.537		0.188	6	−360.525	733.208	2.629	0.036	0.914
0.034	−0.150		−0.113	0.204	6	−360.593	733.344	2.765	0.034	0.948

APPENDIX 7. Model selection results for production of two young per successful pair: Regression coefficients, degrees of freedom (df), log-likelihood, AICc, ΔAICc and Akaike weights for models with a cumulative Akaike weight ≤0.95. The covariates were standardized before model fitting. Models with ΔAICc <2 are considered models with strong support (Burnham & Anderson 2004) and this threshold is indicated by a horizontal line.

— Resultat för val av modell för lyckade häckningar med två ungar: Regressionskoefficienter, frihetsgrader (df), logaritmered sannolikhet, AICc, ΔAICc och Akaike-vikter för modeller med en Akaike-vikt ≤0.95. Variablerna standardiserades inför modellanpassningen. Modeller med ΔAICc <2 bedöms vara modeller med starkt stöd (Burnham & Andersson 2004) och denna tröskel markeras med en horisontell linje.

Intercept	Lake area (km^2) *Areal (km^2)*	Cleared outlet *Rensat utlopp*	Distance to fishing lake (km) *Avstånd till fiskevatten (km)*	Distance to scrub (m) *Avstånd till buske (m)*	df	Log-likelihood *Logaritmerad sannolikhet*	AICc	ΔAICc	Akaike weight *Akaike-vikt*	Cumulative Akaike weight *Kumulerad Akaike-vikt*
−1.152			−0.480	0.271	5	−168.412	347.026	0.000	0.226	0.226
−1.172			−0.546		4	−169.669	347.472	0.446	0.181	0.406
−1.099		−0.990	−0.596		5	−168.874	347.951	0.925	0.142	0.548
−1.099		−0.788	−0.526	0.230	6	−167.908	348.101	1.075	0.132	0.680
−1.154	0.059		−0.491	0.281	6	−168.349	348.983	1.957	0.085	0.765
−1.172	0.010		−0.548		5	−169.667	349.536	2.510	0.064	0.829
−1.097	0.082	−0.841	−0.546	0.242	7	−167.781	349.942	2.916	0.053	0.882
−1.098	0.046	−1.025	−0.609		6	−168.835	349.954	2.928	0.052	0.934