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Ladoga Ringed Seal (*Pusa hispida ladogensis*) Can Breed on Land: A Case Study of the Nursing Period

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ABSTRACT. The ringed seal gives birth and nurses offspring in a subnivean lair in fast ice. Its breeding habitat is transforming under the impact of climate change. Here we report the outcome of an observation of a female freshwater Ladoga ringed seal (*Pusa hispida ladogensis*) and her pup during the 2020 breeding season, when less than 1% of Lake Ladoga was covered with ice. We located a newborn pup in a coastal zone of an island and tracked its survival on land using the camera trap method during daylight. Altogether, we captured 2978 photos, in which the seals were present in 637. The female nursed the pup at the birth site for 34–37 days, which is similar to the lactation period in lairs of the Arctic subspecies (36–41 days, 39 days on average). The female either stayed with the pup or spent time in prolonged aquatic bouts during the day. Percentage of suckling was in the range of 2.4%–4.7% (mean 3.3%, SD = 1.1) on different days. Based on an additional video recording, we found that the pup's behaviour was characterized by a high level of vigilance in comparison with openly breeding phocid seals. This case study indicates that the ringed seal in Lake Ladoga is able to nurse pups on land from soon after birth to pre-weaning. However, breeding success in warm springs can be constrained by predator pressure.

Key words: breeding lair; camera trap; climate change; Lake Ladoga; mother-pup behaviour; pinniped breeding; *Pusa hispida ladogensis*; ringed seal; moulting

RÉSUMÉ. Le phoque annelé donne naissance à ses petits et les nourrit dans un abri subnival de la glace rapide. Son habitat de reproduction se transforme sous l'effet du changement climatique. Ici, nous présentons le résultat de l'observation d'un phoque annelé de Ladoga (*Pusa hispida ladogensis*) en eau douce et de son nouveau-né durant la saison de reproduction de 2020, lorsque moins de 1 % du lac Ladoga était couvert de glace. Nous avons repéré un nouveau-né dans la zone côtière d'une île et avons suivi son évolution sur la terre ferme à l'aide de la méthode du piège photographique à la lumière du jour. En tout, nous avons pris 2 978 photos, et les phoques étaient présents dans 637 d'entre elles. La femelle a nourri son nouveau-né au lieu de naissance pendant 34 à 37 jours, ce qui s'apparente à la période de lactation dans les abris des sous-espèces de l'Arctique (de 36 à 41 jours, pour une moyenne de 39 jours). Pendant la journée, la femelle restait avec son petit ou passait de longues périodes dans l'eau. Le pourcentage de temps consacré à l'allaitement variait de 2,4 % à 4,7 % (moyenne de 3,3 %, écart-type = 1,1) à des jours différents. Un enregistrement vidéo nous a permis de constater que le comportement du nouveau-né était caractérisé par un grand degré de vigilance comparativement à d'autres phocidés se reproduisant dans des lieux exposés. Cette étude de cas indique que le phoque annelé du lac Ladoga est capable de nourrir ses petits sur la terre ferme en commençant peu après leur naissance jusqu'à la période de présevrage. Cependant, le succès de reproduction lors de printemps doux peut être contraint par la pression de prédation.

Mots clés : abri de reproduction; piège photographique; changement climatique; lac Ladoga; comportement mère-nouveau-né; reproduction de pinnipèdes; *Pusa hispida ladogensis*; phoque annelé; mue

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АННОТАЦИЯ. Кольчатая нерпа рожает и выкармливает потомство в подснежной норе на припайном льду. Места её обитания трансформируются под воздействием изменения климата. В сообщении мы приводим результат наблюдения над пресноводным ладожским подвидом кольчатой нерпы (*Pusa hispida ladogensis*), имевшего место в сезон размножения 2020 года, когда лёд покрывал менее 1% площади Ладожского озера. Новорожденный детёныш был найден в прибрежной зоне острова. Мы проследили возможность его выживания на суше при помощи метода фотоловушки. Всего получено 2987 фотографий в светлое время суток, тюлени присутствовали на 637 из них. Детёныш выкармливался самкой в месте рождения 34–37 дней, что по продолжительности близко к периоду

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лактации у арктического подвида в норе (36–41 день, в среднем 39 дней). В течение светового дня самка либо длительное время держалась в акватории озера, либо находилась с детёнышем. Молочное кормление заняло от 2.2 до 4.7% времени (в среднем 3.3%, SD = 1.1) в разные дни. Поведение детёныша отличалось повышенным уровнем беспокойства по сравнению с открыто размножающимися видами настоящих тюленей, по данным дополнительных видеозаписей. Исследование подтверждает способность успешно выкармливать детёнышей на суше у кольчатой нерпы в Ладожском озере с возраста, близкого к рождению, до времени, близкого к прекращению лактации. Однако успешность размножения может быть ограничена в тёплую весну из-за влияния хищников.

Ключевые слова: щенная нора; фотоловушка; изменение климата; Ладожское озеро; поведение самки и щенка; размножение ластоногих; *Pusa hispida ladogensis*; кольчатая нерпа; линька

INTRODUCTION

The ringed seal (*Pusa hispida*) is an ice-breeding phocid seal inhabiting Arctic seas and some aquatic areas in the temperate latitudes, in particular, the Baltic Sea, Lake Ladoga, Lake Saimaa, and the Sea of Okhotsk (Hammill, 2018). Its specific adaptation is giving birth and nursing in a breeding lair, a subnivean construction or cavity in a natural pressure ridge usually located in fast ice. The lair protects the pup from predators and the impact of weather (Lydersen and Gerz, 1986; Lukin et al., 2006).

Breeding in closed lairs left an evolutionary mark on nursing: the lactation period, which is greatly compressed in most true seals, is relatively long in the ringed seal (5–6 weeks). Its milk has a lower fat content and the mother's daily investment is moderate in comparison with studied members of the Phocinae subfamily (Lydersen and Kovacs, 1999). The ringed seal has a small size, so the females have to forage and leave pups for hours (Hammill et al., 1991). Like most ice-breeding species, pups have a lanugo coat at birth (Lydersen and Kovacs, 1999). Weaning is a gradual process since pups usually spend time in the water in the vicinity of females (Smith and Hammill, 1981; Niemi et al., 2013) and consume both milk and solid foods (McLaren, 1958) in the pre-weaning period. Lactation can be extended up to eight weeks (Filatov, 1990; Lydersen and Hammill, 1993) or up to 12 weeks (Niemi, 2013) in different parts of the range, with timing determined in great part by the stability of the ice platform (Lydersen and Hammill, 1993).

Climate change has a great impact on the habitat of the ringed seal due to its influence on the availability of ice and snow for construction and maintenance of birth lairs (Kelly et al., 2010a; Ferguson et al., 2017). Limited ice availability is especially crucial for the landlocked subspecies of the ringed seal, including the Ladoga (*P.h. ladogensis* Nordquist, 1899), Saimaa (*P.h. saimensis* Nordquist, 1899), and Baltic ringed seals (*P.h. botnica* Gmelin, 1788) (Kelly et al., 2010a), because these subspecies have a southern distribution and cannot move northwards. Whether the ringed seal can give birth and nurse a pup on land as a last resort remains an open question (Lydersen et al., 2017). While a report exists of land parturition of the Baltic ringed seal in the Archipelago Sea (Halkka and Tolvanen, 2017), no information on pup survival is available.

The Ladoga ringed seal is a postglacial relict inhabiting Lake Ladoga, the largest freshwater body in Europe (17,891 km^2). It is listed in the Red Data Book of the Russian Federation and has "vulnerable" status in the International Union for Conservation of Nature (IUCN) Red List (Sipilä, 2016). These listings are explained by the restricted range and relatively low abundance of the Ladoga subspecies. Over the 20th century, it declined from 20,000 individuals because of harvesting, which was only banned in 1980. In spring 2012 the number of moulting seals was estimated at about 5000 individuals (Trukhanova et al., 2013), representing a total population size of 6000–9000 (Sipilä, 2016). Besides climate change, threats to the population include becoming bycatch in fishing gear and human disturbance at haul-out and breeding sites (Kunnasranta et al., 2001; Agafonova et al., 2007). In general, the breeding ecology of the Ladoga ringed seal is similar to that of the Arctic subspecies (Kunnasranta et al., 2001). Parturition takes place in late February and early March (Filatov, 1990). It is unknown whether pups of the Ladoga ringed seals can survive in the absence of lairs.

Here we provide the first evidence of successful breeding on land of the ringed seal. We located a newborn pup on an island coast in the northern part of Lake Ladoga in spring of 2020. That spring was extremely mild; ice covered less than 1% of the water area (NASA Worldview, 2020). A complementary purpose of this study was to collect behavioural information. Nursing behaviour of the ringed seal is poorly studied since it is impossible to observe seals in lairs. Our objectives were to (a) find out whether duration of lactation on land corresponds to duration under normal conditions, (b) consider the impact of air temperature and predators on the seals, (c) describe mother-pup behavioural details, activity patterns, and diurnal dynamics, and (d) assess the possibility of monitoring pup moulting using the camera trap method.

METHODS

Study Area and Pup Discovery

We searched for Ladoga ringed seal pups on land in the skerry region of Lake Ladoga in early March 2020. The skerries are a complex of granite islands and islets with an indented coastline in the northernmost part of the lake. Most islands are unoccupied, while there are several inhabited localities on the mainland coast. Some researchers

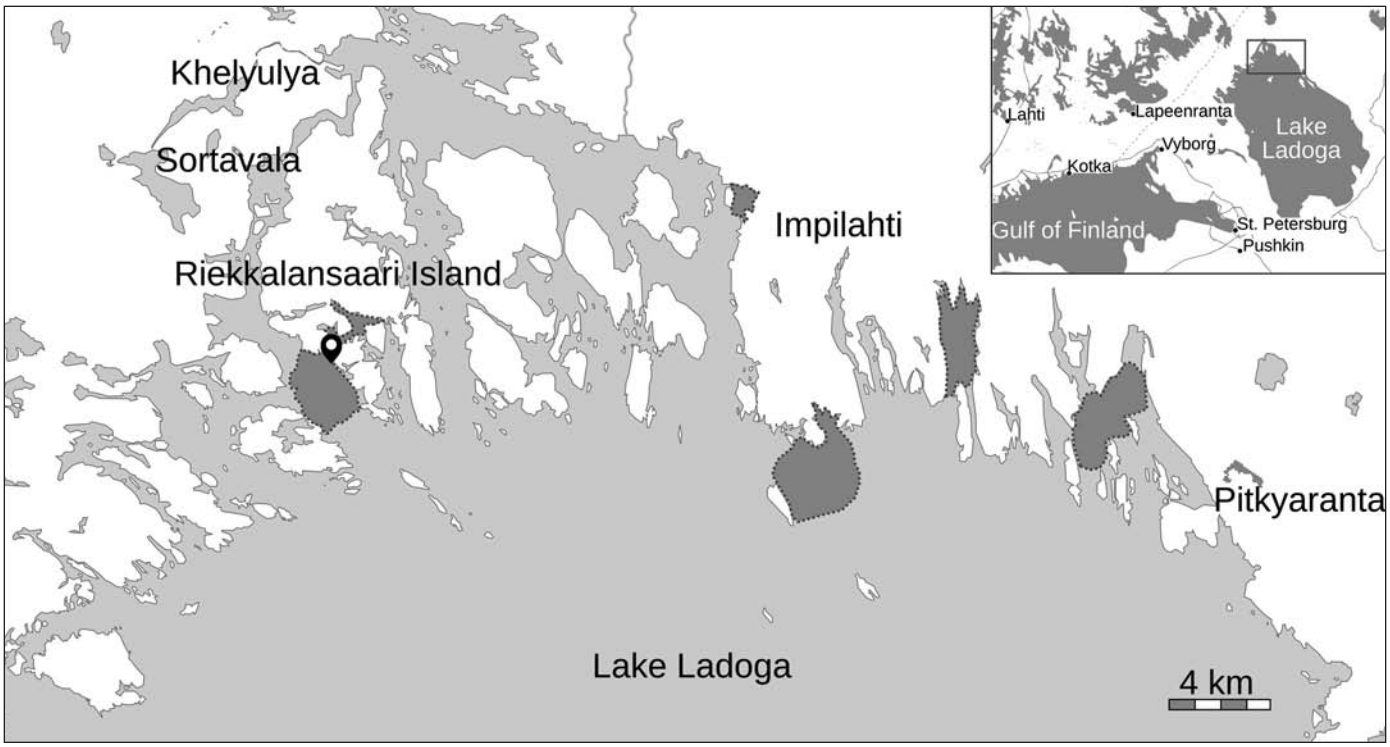

FIG. 1. Surveyed areas (dark grey zones) and the pup's birthplace (location point icon) in the skerry region of Lake Ladoga.

assume that 20% of the seal population winters and breeds in the skerries during the ice season (e.g., Medvedev and Sipilä, 2010). We observed five areas in the Sortavala and Pitkyaranta districts (Republic of Karelia, Russia) (Fig. 1). The observation effort was restricted because of thin or brash ice in most straits and by the seasonal prohibition on boat navigation in the ice-free area.

We found evidence of seal breeding only in the area of Riekkalansaari Island (Fig. 1). A mother with a pup was spotted in a small bay of Pieni Heposaari Island (61˚37′30″ N, 30˚45′32″ E) by drone (Mavic Air 2 Zoom) on 4 March 2020. Because the pup still had the umbilical cord on the day of discovery and blood could be seen at the birth site, we estimated that it was born between 1 and 3 March.

Camera Trap Data Collection

We set a camera trap (LtL Acorn LtL 5210) on a tree at a distance of about 4 m from the nursing site on 15 March and removed it on 20 April when the female was absent. Photos were taken from 06:30 to 20:30 (MSK, UTC+3) at 10-minute intervals (time-lapse system, 85 photos per day), which matched with daylight hours on almost all observation days. The camera's field of view (60˚) captured the coastal ground and the flatter portion of the ledge. We were only able to set up the camera to operate within a limited time frame since we were unable to replace the camera's power source in the course of fieldwork.

The camera trap was in working order for 37 days until we dismantled it, but its functioning was suspended in several cases due to technical failures. In total, 105 photos were lost. This loss made up only 3% of obtained images and was disregarded in the analysis. The number of suitable pictures was 2978.

Camera Trap Data Analysis

We sought to determine the total duration of seal presence at the birth site. Photos were divided into four types: (a) the pup stays alone (female aquatic behaviour), (b) the mother and pup stay together, but no suckling is observed (female haul-out behaviour), (c) the mother and pup stay together and the pup suckles its mother (suckling), and (d) the mother and pup are not seen in the photo. We assumed that if the pup was alone in a photo, the female was absent from the land, since the mother remained in close proximity to the pup and there were no photos with the mother alone on land. We did not attribute to type (b) any photos showing the head of an adult animal protruding from the water, but we discuss these cases.

We reconstructed the female's activity pattern for focal days on which the number of non-empty photos was 60% or more. We estimated the percentage of each state (type of photos) and the number of suckling bouts for each focal day. We define a suckling bout as a single photo or series of consistent photos of type (c) separated by photos of another type. We did not estimate the percentage of (a) photos vs. (b) and (c) photos for the entire period to discover the general activity pattern. It was highly probable that the general proportion of the mother images was overstated since the pup might crawl toward the water's edge (into the camera's field of view) when the mother arrives and move

FIG. 2. The Ladoga ringed seal mother and pup at the birth site on the day of discovery (4 March 2020).

farther inland when she is absent. In this situation, most empty photos would correspond to the pup being alone, while a significant number of cases of the female being in attendance will be captured on camera.

We assessed the influence of air temperature and diurnal changes on the female's activity using the photos captured on all days of seal presence. We took air temperature data (˚C) from the online archive of the Sortavala Weather Station, situated about 10 km from the study site. Meteorological data at the Sortavala Weather Station are recorded every three hours round the clock, and so we used the information obtained from 06:00 to 21:00. The sample was extended with the average temperatures of the adjacent recordings (1.5-hour intervals). We determined the relative proportion of female presence at different temperatures based on series of five photos corresponding to the time of weather recordings (two photos before and two photos after the photo corresponding to the recording).

We estimated for each hour the frequency of female haul-out behaviour, suckling, and total female presence in order to visualize their relative change during daylight. Since the photos were made with a slight time shift (1–2 minutes), we rounded the values accurate to 10 minutes. We performed plotting using R (R Core Team, 2020).

To compare the observed duration of lactation with the duration under normal conditions, we used results for the Arctic subspecies (*P. h. hispida*; Schreber, 1775) taken from harvesting by native hunters (Hammill et al., 1991); we chose these data for their accuracy. We considered the minimum established duration of 36 days to be a necessary and sufficient condition for pup survival. There is evidence of a longer lactation for the Ladoga subspecies (ca. 6–8 weeks) (Filatov, 1990) and the Saimaa subspecies (ca. 9–12 weeks) (Niemi, 2013), but this evidence is mainly rooted in indirect observations; therefore, we did not consider it as a primary basis for the comparison.

We also recorded the pup's moulting process and presence of predators.

Registration and Analysis of Behaviour

We conducted visual observations from the coast of Pieni Heposaari Island on 11–15 March 2020 (15 hours total). We chose a viewpoint on a clifftop 30 m away from the seal site that neutralized the negative impact of the observers. We used a digital Nikon D7100 camera and a 500 mm telephoto lens to take video recordings (114 min) of the mother-pup pair and the lone pup. We described behaviour using the ad libitum approach. In addition, we used continuous recording to process the time budget, with per-second accuracy (Lehner, 1992) for the female during suckling (37 min) and the pup's solitary periods (42.5 min).

RESULTS AND DISCUSSION

Duration of Lactation and Breeding Habitat

The female gave birth on 1–3 March in a narrow bay (13 × 3.5 m) of Pieni Heposaari Island, about 3 km away from the open lake. Based on photographed evidence of bloodstains, the birth site was a small ice platform adjacent to the coast, with no ridges (Fig. 2). The ice platform completely melted between 5 and 10 March, after which the seals stayed on the coast. The seals were recorded for the last time on 6 April (day 23 of the camera trap operation). This means they stayed at the birth site for at least 34 days, possibly for 35–37 days. Two seal heads were photographed in the open water next to each other on the last day, 20 minutes after the seals had lain on the coast.

Lactation duration of the study pair was very close to the duration in lairs of the Arctic ringed seal in Canada and Svalbard: 36–41 days, 39 days on average (Hammill et al., 1991). This suggests that the atypical conditions of land did not affect maternal behaviour in terms of premature abandonment of the pup. Lactation is conceivably longer in the Ladoga subspecies than in the Arctic one (Filatov, 1990), but since the seals left the bay simultaneously, it is possible that the mother nursed the pup for some time after leaving the birth site. Mother-pup pairs of the ringed seal are known to move together or use a mutual home range during the pre-weaning period (Smith and Hammill, 1981; Lydersen and Hammill, 1993; Niemi et al., 2013).

The mother and pup mostly stayed on rocky ground in the deepest part of the bay. Both seals spent much time inland at a distance of several meters from the edge, judging by the direction of their crawling. When the bay froze (20 and 22 March), they used fast ice as a haul-out site. On several occasions, the bay was full of close drift ice, grease ice, or nilas, but the female easily broke these

FIG. 3. Different types of behaviour captured in photos from the camera trap: (a) female aquatic behaviour (the pup stays alone), (b) female haul-out behaviour, (c, d) suckling.

during aquatic trips. The ringed seal normally digs lairs in accumulations of snow in the zone of ice hummocks and ridges of fast ice (Lydersen and Gjertz, 1986; Lukin et al., 2006). However, ringed seals in the northern part of Lake Ladoga use snowdrifts accumulating on ice near the coasts of islands or islets (Kunnasranta et al., 2001). This behaviour probably facilitated the switch to land breeding in warm spring. A narrow bay was a natural alternative to the lair in terms of long-term protection from wave exposure; the lake was frequently rough during the breeding period. Ladoga ringed seals regularly haul-out on land in the open-water season, but they never crawl deep into the coast, preferring the coastal edge, stones in the water, or treeless islets (Agafonova et al., 2007). This means that the female demonstrated considerable behavioural flexibility during the nursing period.

A significant fact is that there were some ice fields in the study area, though the ice was rather thin (10 cm or less) and did not reach the bay. The ice eventually became thinner and broke during thaws. In early March we found two seal pups on these ice fields. Thus, parturition in the coastal zone was an individual strategy of the female. Nothing like this has been observed in the harp seal (*Phoca groenlandica*) in the Northwest Atlantic, which never gives birth in the coastal zone, even if the ice quality is poor (Stenson and Hammill, 2014), and we identified no related information for the other obligate ice-breeding species of the true seal family.

Pattern and Diurnal Dynamics of Seal Activity

The seals were present in 637 photos (35%) taken during their stay at the birthplace. The camera trap provided 408 photos of the pup staying alone (female aquatic behaviour), 185 photos of the mother and pup staying together (female haul-out behaviour), and 44 photos of suckling (Fig. 3). There were no images of animals in 1193 photos, including photos taken on four consecutive days (31 March–3 April). According to image data, the female visited the pup every day. Two different patterns of female activity were recorded on the focal days in daylight: either the female was mostly absent from the site (82.4%–96.4% of the time) or mostly

TABLE 1. Activity pattern of the female on different dates of camera trap operation (March and April 2020).

Data	% Female aquatic behaviour	% Female haul-out behaviour	% Suckling	% Female presence (haul-out and suckling)	Number of suckling bouts	Number of seal photos per day	% Seal photos per day of 85
15 March	82.4	9.8	7.8	17.6	3	51	60
20 March	83.8	13.2	2.9	16.2	2	68	80
21 March	92.6	4.9	2.5	7.4	1	81	95
23 March	91.0	4.5	4.5	9.0	2	67	79
26 March	20.4	72.2	7.4	79.6	2	55	65
28 March	0.0	96.7	3.3	100.0	2	60	71
29 March	94.5	1.8	3.6	5.5	1	54	64
30 March	96.4	1.2	2.4	3.6	1	83	98
06 April	0.0	92.5	7.5	100.0	2	53	62

stayed with the pup (79.6–100% of the time) (Table 1). The percentage of suckling varied from 2.4% to 7.8% on a given day. Of note, the percentage of photos with suckling was inversely correlated with the total number of seal photos per day ($r_s = -0.92$, $p < 0.05$), which indicates that most suckling bouts took place in front of the camera. Therefore, we also calculated the percentage of suckling from the total number of photos per day. Suckling made up between 2.4% and 4.7%, the mean being 3.3% ± 1.1 SD. No daily trends in the percentage of suckling were established with the use of the linear model. The pup reliably stayed alone from 10 minutes to 8 hours, while the female reliably stayed with the pup from a few minutes to 9 hours, 40 minutes.

Ringed seal females normally feed during lactation. In general, they spend little time on ice (16%–24%), as shown in telemetry studies (Kelly and Quakenbush, 1990; Lydersen and Kovacs, 1999; Kelly et al., 2010b). In this case study, the female's presence on land was not restricted by the costs associated with maintaining breathing holes in ice (Smith and Hammill, 1981) or by the air capacity of the lair chamber (Lukin et al., 2006). This is probably the reason why she stayed with the pup for the entire day at least twice. The proportion of suckling during daylight was close to the data reported for the harp seal (Kovacs, 1987a) and the grey seal (Kovacs, 1987b; Smiseth and Lorentsen, 1995), though these species use the strategy of more rapid energy investment in the pup (Lydersen and Kovacs, 1999). It can be assumed that the female fed the pup 3–4 times in 24 hours.

There were no indications that the pup left its birthplace before 31 March. The females of the Arctic and the Saimaa subspecies can make several lairs, and pups swim between them (Smith and Stirling, 1975; Sipilä, 1990). At the same time, they actively keep to the lair sites, even if the snowdrift melts (Smith and Hammill, 1981; Auttila, 2015). Loss of pups during their swims when open water occurs is one potential threat. The attachment of the pup to the birth site in the absence of physical barriers (lair walls or hole in the ice) might have prevented the loss. That is, this attachment contributed to mother-pup reunions in the same location after the female's aquatic trips.

The female's haul-out behaviour had a clear daylight dynamic, with a symmetrical rise and fall and the maximum occurring at ca. 13:00. Suckling could take place at almost any time of day. In general, female presence increased in the morning, had a spike at ca. 12:00, and fell steeply after 19:00, when she was usually absent (Fig. 4). The female's daytime activity agrees with the behaviour of ringed seals from different areas in spring (Stirling, 1977; Lydersen, 1991; Järvinen and Sipilä, 1992). This behaviour has previously been attributed either to diurnal prey migration (Stirling, 1977) or to light and temperature peaks (Lydersen and Hammill, 1993).

Impact of Air Temperature and Predators

Air temperature varied from –9.1 to 11.2˚C during daylight (camera trap operating time), and from –9.6 to 7.5˚C during the period when seals stayed at the birthplace. We considered data from 67 temperature recordings and 329 seal photos. The female tended to stay with her pup at positive air temperatures; namely, the proportion of photographs with the female present was 85.0% at air temperatures 3˚C and above, as compared to 18.0%–25.7% at lower values (Table 2).

Stable microclimatic conditions in the lair protect pups of the ringed seal during the lactation period. Air temperature in the chamber is considered to maintain at around 0˚C, according to the law of heat transfer (Smith and Stirling, 1975; Lukin et al., 2006). In the case we observed, while fluctuations of air temperature had no vital effect on the pup, they appeared to influence the female's haul-out behaviour. For the harp seal, there is a hypothesis that lactating females defray some thermoregulatory costs by spending time in the water at low air temperatures, since temperature drops affect metabolic rate (Perry et al., 2017). However, for the ringed seal, a female's attendance with her pup may be a guarantee of the pup's security from medium-sized predators, such as some birds (Lydersen and Smith, 1989; Järvinen and Sipilä, 1992). If other females of the Ladoga seals show a similar response to air temperatures, we can speculate that low temperatures indirectly affect pup survival because of an increased risk of attacks on cold days. We may also suggest that, in this specific case, the lack of precipitation contributed to the pup's survival.

Two occasions of predator presence were recorded. The camera trap captured the presence of a White-tailed Eagle (*Haliaeetus albicilla*) perched on a rock about 3–4 m

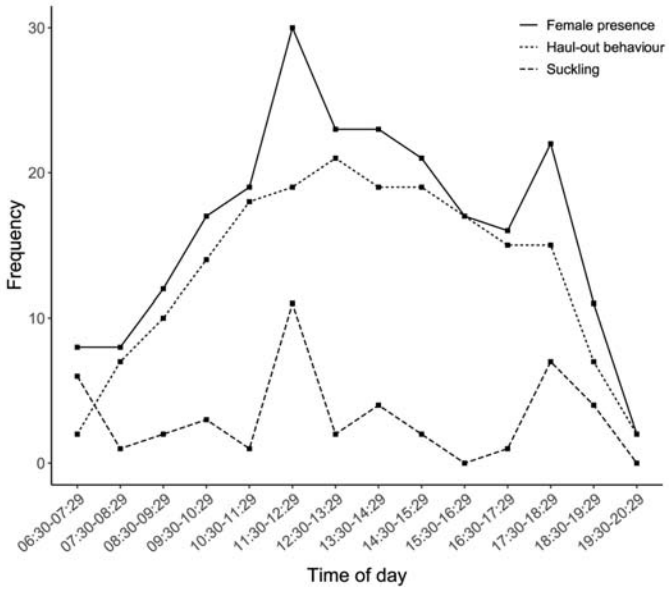

FIG. 4. Daylight dynamics of suckling, female haul-out behaviour, and total female presence. The top line displays the sum of the two lower lines.

from the lone pup resting on fast ice (Fig. S1). The pup was captured by the camera on the following day with no injury or other indications of an attack. An American mink (*Neogale vison*) was recorded on the shore on 23 March; the seals were absent in that photo. In northern Lake Ladoga, red foxes (*Vulpes vulpes*) and wolves (*Canis lupus*) occasionally catch seal pups (Kunnasranta et al., 2001), but these predators were not recorded. There is an anecdotal report of an American mink predating on a neonate harbour seal (*Phoca vitulina*), but this is not typical for mink (Clark et al., 2016). White-tailed Eagles prey on pups of the Baltic ringed seal (Halkka and Tolvanen, 2017) and the Baltic grey seal (Jüssi et al., 2008), especially in mild springs.

A curious note is that the first recording of the eagle in the study area was on 12 March, while the eagle reliably spotted the pup only after 10 days and only when the bay froze. The pups of the Ladoga ringed seal have relatively dark hair, namely cream or brown (Agafonova et al., 2007). The brown hair of the observed pup camouflaged it well on granite. In contrast, the pups on the ice substrate were fairly noticeable. The priority task of future research will be to investigate whether hair colour plays a role in the selection of pups by avian predators, depending on substrate type and whether a dark coat favours land breeding.

Mother-Pup Communication and Behaviour Details

We conducted our visual observations when the pup was 1.5–2 weeks old. The pup was seen both with its mother and alone. When the female returned, brief naso-nasal contact took place. After each coming ashore, even after short divings, she scratched the pup with her forelimb for three to four minutes. The pup rolled from side to side during these sessions, scratching itself and tapping the mother with its own forelimb. Once, the female stopped

TABLE 2. Relative proportion of photographs with the female from the total number of seal photos at different air temperatures values.

Air temperature, °C	% Female photos	Number of seal photos
< −3	18.0	50
−3 to −0.1	25.7	71
0 to 2.9	23.6	148
> 2.9	85.0	60

scratching after the pup bit her face. Published data on mother-pup communications of the ringed seal are very scarce. Some observations indicate that Arctic ringed seals also communicate with pups through nuzzling contact and flipper scratching (Smith and Hammill, 1981).

The female adopted a side pose before suckling. Suckling bouts varied between nine and 22 minutes, the longest consisting of two acts (13 and seven minutes) with a two-minute interruption. During suckling, the pup alternated nipples every two to 46 seconds (9.4 ± 8.5 SD seconds, on average) without any significant pause between sides. While the pup was suckling, the female usually kept her head down and had her eyes closed (66.5%), but often puffed out her nostrils. Occasionally she scanned the surroundings (26.7%), changed her body position (1.9%), or put her head under water (4.9%).

During haul-out bouts, the pup mostly stayed at a distance from its mother of less than its body length. Both animals occasionally stuck out their tongues. We recorded no other apparent communication contacts. On 11 March the female demonstrated unusual behaviour: while lying on the rocky ledge, she moved her hindlimbs rapidly from left to right, making gestures as if she was rubbing the limbs together. This movement lasted several seconds and was repeated a few times. After the last occasion, the pup, which had crawled away, moved back to the mother. The observed behaviour might be a signal for the pup to approach the mother or an unknown comfort reaction associated with the cold season. Female harbour seals, which move a lot in the sea with their pups, have a number of visual signals to encourage following behaviour (Wilson, 1974).

The female left the shore gradually, first staying in the water of the bay for several minutes. The pup emitted brief vocal calls in these moments. We did not record any vocal behaviour on the part of the female.

The pup usually lay still (42.6%) while it stayed alone, mostly on its side, but sometimes on the back or abdomen, or it hovered in a vertical pose for a minute. The pup often scanned the surroundings (22.8%) and sniffed the air. It also spent a lot of time on comfort behaviour (31.2%) (visible in Fig. 3a), which was represented by a full set of reactions characteristic of an adult individual (Agafonova et al., 2007): yawning, stretching the body or front flipper, fan-shaped spreading of hind flippers, head or face rubbing, and changing the position of the body or hind flippers. The pup also demonstrated some infant reactions: wriggling on its back and stretching (the pup stretched its face

towards the hind flippers over its back, lying on its side). A few times, the pup rolled from side to side and waved its limbs while lying on its back (0.2%). On 12 March it trembled a lot. Trembling is a usual phenomenon for wet lanugal pups (Smith and Hammill, 1981; Kovacs, 1987a) associated with the underdevelopment of the blubber layer and the thermogenesis process (Kovacs, 1987a). The pup moved little (3.2%), but empty photos from the camera trap indicate that it might have changed position many times a day.

In general, the pup spent much more time scanning than is usual for pups of studied "open-breeding" species of Phocinae (1.3%–6.5%) (Kovacs, 1987a,b; Rosen, 1990). A high level of vigilance may be an important part of antipredator behaviour for pups of the ringed seal when they are reared outside a lair.

We made some additional notes on the basis of camera trap images. Joint swimming in the bay was recorded four times between 21 March and 4 April (from an age of 18–20 days) (Fig. S2a). The pup had wet fur five more times after 20 March, which indicates that its swimming activity could have been even greater. Once, directly after joint swimming, the pup suckled from its position in the water while the mother lay on the shore (Fig. S2b). The ability of pups of the ringed seal to swim at the stage of lanugo coat evolved in the Arctic as a response to strong predation pressure (Lydersen and Hammill, 1993). No cases of swimming without the mother were recorded. Ladoga ringed seals probably teach pups to swim, as shown in some other seal species (Kovacs, 1987a).

Based on photos taken by the camera trap, a visit of a stranger adult seal was recorded (Fig. S3). The seal tried to come out of the water when the female was staying with the pup. The response of the female was unclear. We visually observed adult seals near the bay on 11–15 March, but they did not attempt to go ashore. Females of the ringed seal are territorial during the lactation period, expelling other individuals from the vicinity of lairs until weaning (Smith and Hammill, 1981; Niemi et al., 2019). The same behaviour probably persisted in the case of land breeding. In camera trap photos (n = 16), a seal's head was also seen with the lone pup, but it remains unclear whether this was the mother or a stranger seal. Mothers of some seal species watch pups from the water, which increases the pups' chances of survival (Kovacs, 1987a; Smiseth and Lorentsen, 1995).

Monitoring of Pup's Moulting

The first indication of the pup's moulting was recorded in photos on 21 March, when the lanugo coat started to fall from its face and the forelimbs (See Fig. S4a–d, where moulting is visible over a span of 16 days). The first bald spot at the back of the head was recorded on 25 March. In photos from 26 March, a large spot is visible on the pup's chest between the forelimbs. Small spots on the abdomen were also visible, whereas the back remained covered. On 28 March a slight trace of moulting of the hindlimbs was recorded. There was a gap in seal photos between 31 March and 3 April. By 5 April, half of the pup's back was moulted, and by 6 April two thirds of the back were moulted. The lanugo coat remained on the more caudal part of the body and the hind flippers. The moulting process continued for 17 days, from the 18th to the 34th day from the date of the pup's discovery, and was not completed when the pup left the site. The beginning of moulting at the pup age of 2–3 weeks agrees with previous knowledge on *P. h. hispida* (Hammill, 2018).

In lanugal pups of the harp and grey seal, moulting normally starts around the facial area and flippers, followed by the abdomen and back. In starveling pups, moulting occurs in reverse order. Such pups experience cold stress because of the lack of insulating blubber and have to mobilize responses to prevent heat loss (Lydersen et al., 2000). While we could not measure the body mass of the pup, the order of its moulting seems to indicate that it experienced no considerable cold stress.

CONCLUSION

Our case study showed that the pup of the Ladoga ringed seal was physiologically able to develop on land, and that its mother expressed appropriate behaviour over the nursing period under atypical conditions. Climate change affects marine animals by decreasing the stability of the environment (Doney et al., 2012), and further adaptation of a species depends on its ecological plasticity. The ringed seal is considered an obligatory pagophilic animal. It has a number of traits adapted to the stable conditions of the breeding lair (Lydersen and Kovacs, 1999). Although there are reports of partial or complete nursing by the ringed seal on open ice (Heptner et al., [1976] 1996; Lydersen and Hammill, 1993; Lukin et al., 2006; Auttila, 2015) and even the completion of nursing on rocks (Auttila, 2015; Halkka and Tolvanen, 2017), some researchers, including Lydersen et al. (2017), have suggested that the terrestrial substrates are unlikely to replace the nursing habitat because of thermal challenges and predators, at least at high latitudes. In our case, nursing on land presumably became possible owing to traits of the pup, such as an attachment to the birth site and a high level of vigilance, combined with an early ability to swim, as well as the dark colour of the lanugo coat camouflaging the pup on granite. These traits may play a role in the defence against avian or mammalian predators. We can also conjecture that the island coasts are more favourable for breeding than open ice since they provide better shelter. It is clear that all these assumptions should be tested on a large sample.

The skerry islands in the north of Lake Ladoga look like a suitable region for seal breeding on land. Unfortunately, we have no information about the number of Ladoga ringed seals breeding on land in 2020 or the survival rate of the pups. Despite the positive outcome recorded in our study, predators remain a serious threat to pups in the absence of a

lair, though the degree of this threat can vary greatly under diverse circumstances.

Further research into the breeding ecology of the Ladoga ringed seal subspecies in mild spring should proceed in two directions: first, one should determine the proportion of females nursing in different habitats and their breeding success; second, one should record pup development and maternal behaviour based on a large number of individuals. Models of the environmental impact on mother attendance must include pup age, air temperature, and other meteorological factors, such as wind speed, relative humidity, cloudiness, precipitation, wave height, and current ice state near the birthplace. Extensive research of this kind will shed light on the future of the Ladoga subspecies under conditions of climate change and contribute to the elaboration of relevant conservation measures.

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