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Breeding behavior and pup development of the Caspian seal, *Pusa caspica*

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The Caspian seal, *Pusa caspica*, is an ice-breeding phocid endemic to the Caspian Sea. The breeding behavior of this species is poorly documented. Here, we report behavioral observations of 518 mother–pup pairs (MPs) and 210 lone pups (LPs), made from the bridge of icebreakers traversing seal breeding grounds while servicing oil installations in the northeastern Caspian Sea, during 34 trips from late January to early March, 2006–2012. The breeding habitat of Caspian seals is land-fast or drift ice, usually at least 20 cm thick, overlying water 3–5 m deep. Pregnant females formed pairs or small groups. They were not observed to use lairs, but preferentially pupped beside ice ridges or ice-slab piles that afforded shelter to pups. In years when there were few natural leads into the ice-field, females often gave birth on the edge of artificial leads formed by shipping channels. Pups were categorized into stages from 1) newborn, 2) white-coat, 3) molting, and 4) molted, with stage 3 and 4 pups appearing from mid- to late February. The nursing period lasted at least 3 weeks and neighboring MPs appeared to be mutually tolerant. Mothers left their pups alone or at nursery sites, presumably to forage. Most white-coat pups moved over the ice while avoiding water in response to disturbance from vessels. MPs maintained contact while moving across the ice by a combination of the pup's following response and diligent chaperoning by the mother. During disturbances, some LPs sought refuge in shelters under ice slabs, whereas others followed a neighboring MP away from the vessel. Male–female pairing occurred in late season with no male–male competition observed on the ice. While breeding and pup-rearing behavior of Caspian seals has some features in common with that of other Holarctic seals, it is largely distinct and adapted to the unique conditions of the Caspian environment, in particular the paucity of snow cover on the ice.

Key words: breeding behavior, breeding habitat, Caspian Sea, ice-breeding, Kazakhstan, phocid, pinniped, *Pusa caspica*, seal pup development

The Caspian seal, *Pusa caspica*, is a small-bodied, ice-breeding phocid with minimal sexual dimorphism. Asymptotic adult body length (ABL), in both sexes, is approximately 130 cm (Wilson et al. 2014), similar to the Arctic ringed seal, *Pusa hispida* (Krafft et al. 2006). Genetic data indicate a divergence from an ancestor shared with gray (*Halichoerus grypus*) and ringed seals 1–2 million years ago, after which it evolved independently to become a distinct species, endemic to the Caspian Sea (Fulton and Strobeck 2010; Nyakatura and Bininda-Emonds 2012). Despite a history of commercial exploitation spanning more than 200 years (Härkönen et al. 2012), very little is known about its ice-breeding behavior and pup development. The Caspian seal is believed to be a single panmictic population ranging throughout the Caspian Sea outside the breeding season. Animals begin to return to the north Caspian in late summer and move into the winter ice-field when it forms in late December (Fig. 1; Krylov 1990; Dmitrieva 2013; Dmitrieva et al. 2016). Most pups are born on the ice surface between late January and the 3rd week in

February, with a peak of newborn pups observed from the vessels around the 2nd week in February. Newborns are approximately 5 kg (Krylov and Vorozhtsov 1972; Popov 1982) with a long, dense white lanugo coat. Pups gain weight at 0.5–0.8 kg day per day, with the body weight of molting and molted pups ranging from 15 to 23 kg (Roganov 1932).

This paper presents a summary of observations made during 2006–2012 of Caspian seal mothers and pups on the winter ice-field in the northern Caspian Sea. Observations were made from the bridge of icebreakers transiting the breeding area while servicing oil industry installations. Although the original objective was to record the responses of mothers and pups to icebreakers to develop mitigation for shipping disturbance, our observations of breeding habitat, behavior, and pup development are the first for this little-known species.

Materials and Methods

Observations of seals on ice were made from the bridge of icebreaking vessels servicing oil industry installations in the northeastern Caspian Sea between 2006 and 2012. Vessels travelled between the Kashagan field and Bautino through land-fast or drift ice overlying water depths of 3–5 m (Fig. 1). Sampling was opportunistic, determined by operational constraints on vessel access, scheduling, and routing. The annual observation period was divided into early season (27 January–9 February), mid-season (10–19 February), and late season (20 February–6 March). A total of 34 transits were made with observers on board, but it was not possible to cover each part-season in every year (Table 1). Therefore, some observations are referred to by specific season or transit in the text. Most transits took approximately 2–3 days, depending on ice thickness and operational requirements. Breeding seals were most often encountered between Kalamkas field and the ice edge (Fig. 1; Härkönen et al. 2008). Vessel speed during observations ranged up to 8 knots.

The behavior of seals ahead and to the side as the vessel passed was recorded by 1–2 observers on each side of the bridge using binoculars, voice recorders, digital cameras, and notebooks. Distance of seals within a strip of 0–200 m from the side of the vessel was measured by laser rangefinders, range-finding binoculars, or visually for seals very close to

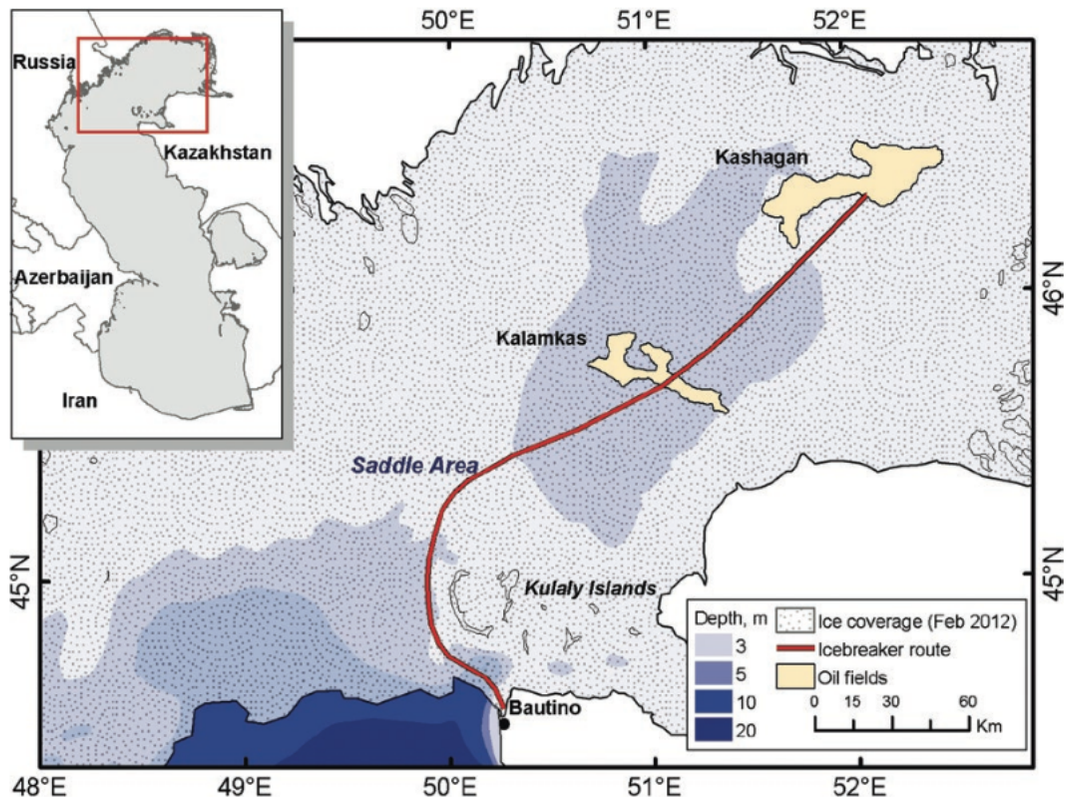

Fig. 1.—Study area in the northern Caspian Sea and the route of icebreakers from which observations of ice-breeding behavior of Caspian seals (*Pusa caspica*) were made.

Table 1.—Number of icebreaker transits (1 way) by season and year during which records of breeding behavior of Caspian seals (*Pusa caspica*) were made in the northern Caspian Sea.

	2006	2008	2009	2010	2011	2012
Early season (27 Jan.–9 Feb.)	0	0	2	2	0	4
Mid-season (10–19 Feb.)	0	2	0	1	4	5
Late season (20 Feb.–6 Mar.)	1	1	3	1	2	6

the vessel. An adult lying beside a pup was assumed to be its mother and an adult followed by 2 or more pups was assumed to be the mother of one of them, usually the pup closest to her. Overall, the behavior of 518 focal mother–pup pairs (MPs) and 210 lone pups (LPs, i.e., pups whose mothers were not visible) was recorded (Table 2), and the distance to focal animals was recorded in most cases (Table 3; Supplementary Data SD1). The distance between mother and pup or MPs was estimated in ABL, with 1 ABL approximately equal to 1 m. Stages of development of 1,448 pups, noted as either in MP pairs or as LPs, were recorded visually and photographically (Supplementary Data SD2 and SD3). We defined stages of development 1–4 for Caspian seal pups based on designations for harp (*Pagophilus groenlandicus*) and gray seal pups (Kovacs and Lavigne 1986; Kovacs 1987a, 1987b). Caspian seal pups have a white lanugo coat for at least 3 weeks after birth (Supplementary Data SD2). The coat of neonatal pups has a yellowish tinge once the birth fluids have dried (defined as stage 1). The yellowish tinge wears off, leaving a covering of white lanugo, while pups grow from small and thin (early stage 2), to being large and fat (late stage 2). From late stage 2, the lanugo begins to molt from the hind flippers and face. Stage 3 is reached when molting begins around the tail. Stage 4 pups are fully molted and the lanugo is replaced by a new coat that is pale silvery gray dorsally and white ventrally (Supplementary Data SD2). Lone adults (LA), defined as adults with no accompanying pup, were recorded in early and late seasons at distances up to approximately 400 m.

Statistical analysis and data visualization were carried out using the R statistical package (R Core Team 2016).

Table 2.—Total number of Caspian seal (*Pusa caspica*) pups recorded in mother–pup pairs (MPs) and as lone pups (LPs) from (a) the photo record and (b) the behavioral record (Supplementary Data SD1). Data from the northern Caspian Sea, 2006–2012.

	Number of MPs	Number of LPs
Early season (27 Jan.–9 Feb.)		
(a) Total record	73 (61.3%)	46 (38.7%)
(b) Behavioral record	42	9
Mid-season (10–19 Feb.)		
(a) Total record	296 (54.2%)	250 (45.8%)
(b) Behavioral record	176	81
Late season (20 Feb.–6 Mar.)		
(a) Total record	490 (61.8%)	303 (38.4%)
(b) Behavioral record	300	120

Table 3.—Number of focal mother–pup pairs (MPs) and lone pups (LPs) of Caspian seals (*Pusa caspica*) for which behavior was recorded in each distance band from the side of the vessel. Data from the northern Caspian Sea, 2006–2012.

Distance band (m)	MPs	LPs
0 to < 10	67	96
10–49	35	77
50–99	17	17
100–199	16	19

Results

Pre-pupping adult groups.—In late January, LAs were frequently seen swimming either in open-water sections of the shipping channel or in polynyas. During 2 transits in late January 2009 and 1 in 2010, 30% of 133 and 35% of 65 LAs, respectively, were seen in the pre-existing open-water channel ahead of the vessel with the remainder in natural polynyas. During 1 transit in late January 2012, all of the 203 LAs observed were in the open-water channel ahead of the vessel.

Across all years only small numbers of LAs were seen hauled out during late January, either singly or in groups. Most of the animals in these groups had body shapes characteristic of pregnant females. In late January 2009, 14 LAs were recorded as hauled out singly, 13 at the edge of polynyas and 1 on the shipping channel edge. Five adult dyads, 1 triad, 1 group of 6, and 1 group of about 16 adults were hauled out at the edge of polynyas. In late January 2010, 12 LAs were recorded as hauled out singly, 7 along the shipping channel edge, while 3 dyads were noted, 1 on the channel edge.

Birth and nursery site characteristics.—Birth sites of Caspian seals were identified by blood-stained areas of ice. Nursery sites, surrounding birth sites, usually included deformities in the ice, such as ridges or stacks of ice slabs, which can provide shelter to pups from the wind (Fig. 2). Adults entered the water either through access holes that they created

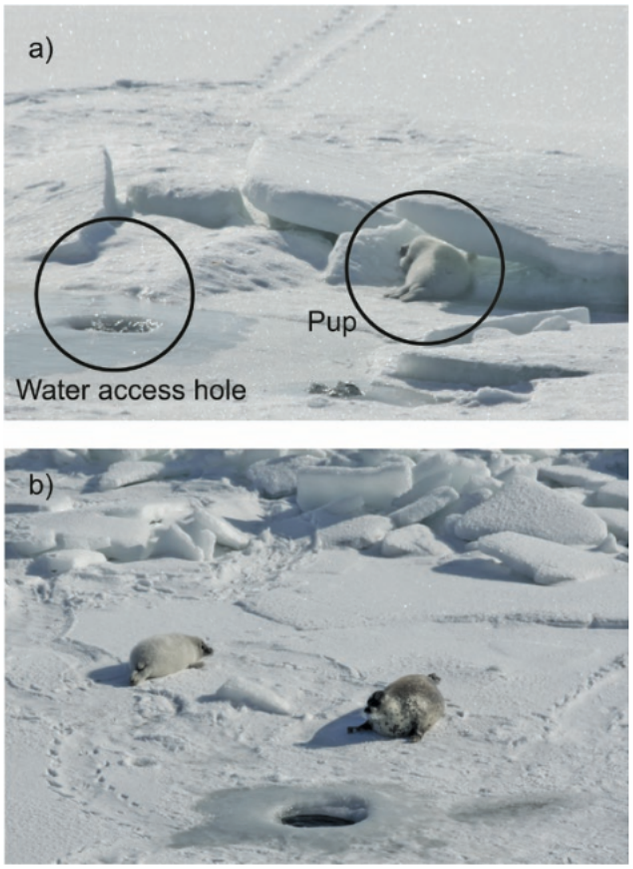

Fig. 2.—Nursery sites of Caspian seals (*Pusa caspica*): a) a lone pup using an ice block for shelter with an access hole nearby, b) a mother–pup pair in typical ice ridge nursery habitat adjacent to the access hole.

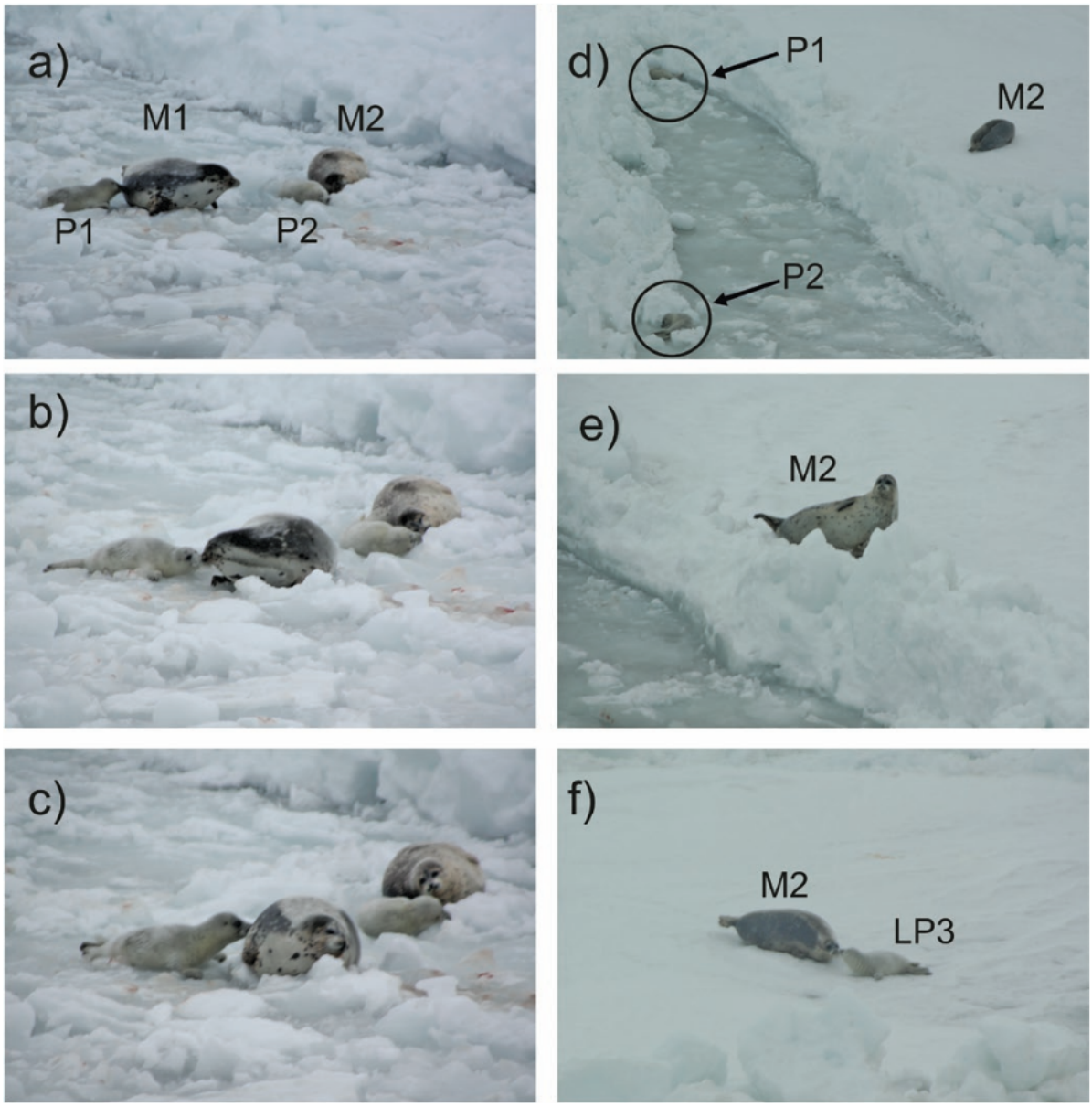

Fig. 3.—Time series of 2 adjacent mother–pup pairs of Caspian seals (*Pusa caspica*) showing: a) pup 1 seeking nipples, b) mother–pup 1 nose contact, c) pup 1 suckling, d) M1 departed, M2 climbed on to a ridge overlooking pups 1 and 2, both resting, e) M2 in an alert stance, and f) M2 makes nose contact with an unknown lone pup that approached her.

and maintained or via an adjacent polynya or shipping channel. Adjacent MPs could be as close to each other as ~2 m (Fig. 3).

Most nursery sites were on ice 20–40 cm thick. Pups between stages 2 and 4 were frequently noted beside birth sites and established nursery site structures, suggesting that pups were sedentary throughout much or all of the nursing period. In 2006, 2010, and 2012, females used the edge of the vessel channels as birthing sites. In 2006, the ice sheet formed very rapidly at freeze-up, and few natural leads formed in the ice; these conditions resulted in large numbers of females using the icebreaker channels (Härkönen et al. 2008), and 154 of 263 (59%) MPs within the 200-m observation strip were recorded within 10 m of the vessel (Supplementary Data SD1). In comparison, during 2010, the icebreaker channels were used mainly by small numbers of late-arriving females. On 19 February 2010, only 17 pups were recorded along a pre-existing vessel channel edge for a total length of about 10 km.

Pupping habitat ice type.—From the photographic record, 163 MPs (61%) were located in ice-rubble fields, whereas 105 (39%) were on mainly featureless ice sheets (Supplementary Data SD1). The latter includes 79 records from 25 February 2006, made between "the Saddle" area and the ice edge (Fig. 1), where ice-rubble habitat was rare in the vessel corridor during that season.

During the 2008 transits, when new channels were being forged through the ice-field containing both ice-rubble fields and featureless flat ice habitat, a total of 17 MPs (77%) were identified at deformed ice features, whereas only 5 (23%), all single MPs, were seen on flat ice. All 7 groups of 2 or more MPs for which the habitat was recorded were beside ice features.

During the 2010 and 2011 transits, ice-rubble fields containing MPs were encountered frequently. Adjacent nursery sites

were often separated by ice ridges, partially or completely surrounding a pan of smooth ice. MPs photographed on a transit through rubble-field habitat on 23 February 2011 (late season) were all at least 5 m apart, 44% (31 of 70) interpair distances were 10–20 m apart, 16 (23%) were > 20 m apart, and 6 (9%) were at distances > 50 m apart.

Pup development and maternal attendance.—The relative abundance of pups at each developmental stage varied through the observation period (Fig. 4; Supplementary Data SD3). Based on counts across all years, stage 1 pups were most abundant in the early season, with 70% of stage 1 records occurring before mid-February (Fig. 4b). Stage 1 pups continued to be observed at low frequency through the end of February, indicating the presence of some late-breeding females (Figs. 4c and 4d). Stage 1 pups recorded in mid- and late seasons were observed along the edges of icebreaker channels, which had been colonized by late-coming pregnant females.

Stage 2 pups were seen in all periods, but their frequency increased rapidly from the 2nd week of February, with peak

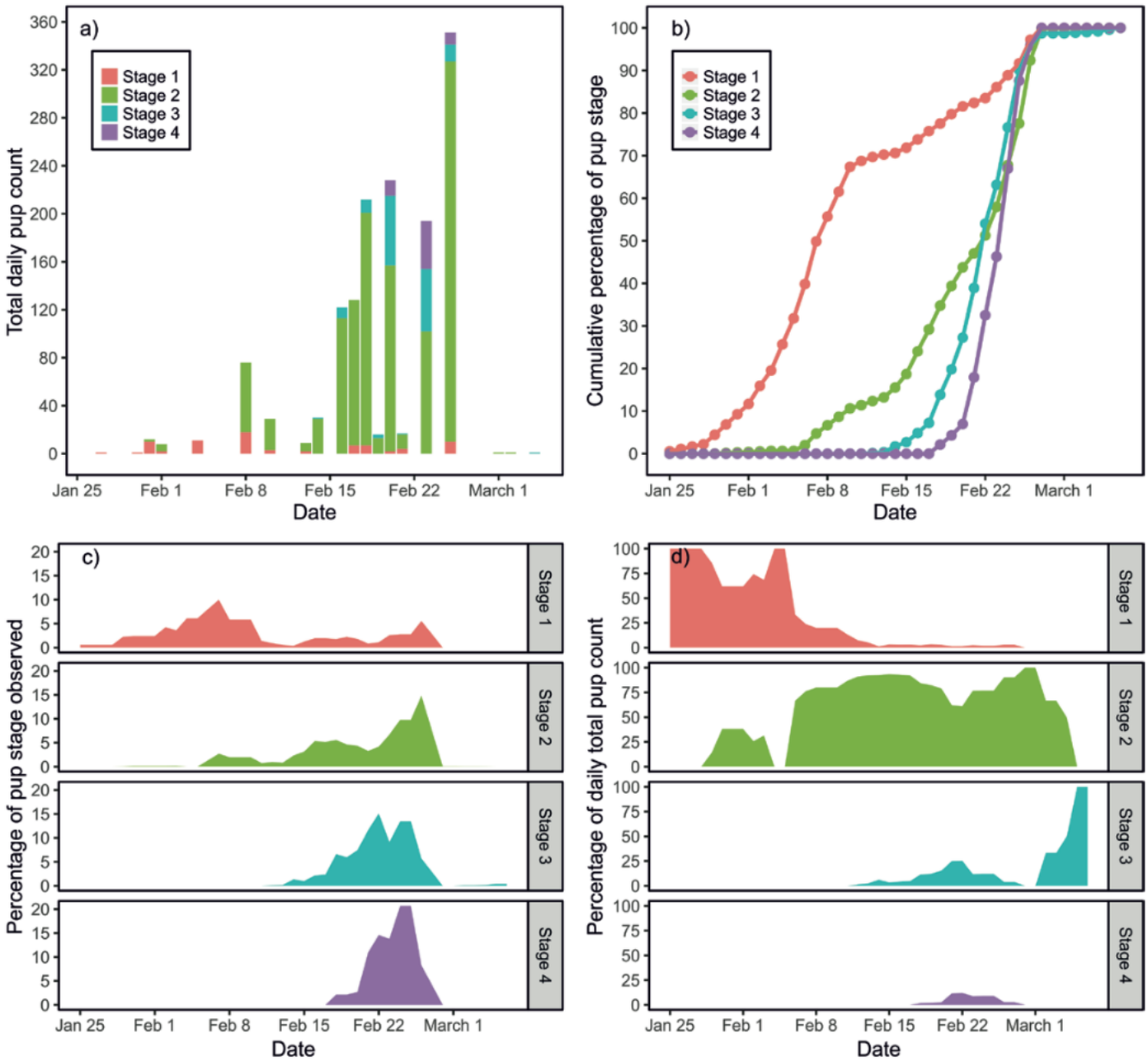

Fig. 4.—Temporal distribution of developmental stages of pups of Caspian seals (*Pusa caspica*): a) histogram of total daily pup counts over all years (2006–2012) by developmental stage (data from Supplementary Data SD3); b) plot of the cumulative percentage of each pup stage observed by date; c) plot of the percentage of each pup stage observed by date; d) plot of percentage of daily pup count represented by each stage versus date. Plots b–d were calculated on the basis of a 5-day "sliding-window" average of total daily pup count across all years 2006–2012, with 1-day increments, for the period 25 Jan.–6 Mar. This approach was used to estimate smoothed temporal pup stage distributions from the sparse, variable daily pup count data available. Early season: 27 Jan.–9 Feb.; mid-season: 10–19 Feb.; late season: 20 Feb.–6 Mar.

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Supplementary Data

Supplementary Data SD1. Data table in text ".csv" format containing information on observations of focal mother–pup pairs and lone pups.

Supplementary Data SD2. Figure showing photographs of developmental stages of Caspian seal pups.

Supplementary Data SD3. Data table give counts of developmental stages of pups versus season period based on observations extracted from photographic logs.

Supplementary Data SD4. Figure showing examples of aversion to water by white-coated (lanugal) Caspian seal pups.

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For Caspian seal pups born in the 3rd week in February, lactation might be as short as 2 weeks in years with early ice melt, but the survival of such late-born pups is not known.

Mother and pup behavior.—Most of the movement of MPs in this study occurred in the context of the seals moving away from an approaching icebreaker. However, in undisturbed conditions Caspian seal pups appear to be sedentary, remaining close to their birth site until the ice melts. Sedentary behavior is also characteristic of harp and gray seals (Lydersen and Kovacs 1999), which move only a few meters for suckling (Kovacs 1987a). The Caspian seal pup's strong following response to its mother and the mother's diligent chaperoning behavior are typical of other phocid seals, including harbor seals (*Phoca vitulina*) both onshore (Renouf and Diemand 1984; Lawson and Renouf 1987) and in the water (Wilson 1974; Wilson and Kleiman 1974; Lawson and Renouf 1987). For example, harbor seal mothers fleeing disturbances wait for, or return to, their pups if they fall behind (Lawson and Renouf 1987).

LPs and maternal foraging.—Maternal foraging is thought to be necessary for small-bodied phocids that cannot store sufficient energy to support lactation. A maternal strategy of alternating periods of nursing and foraging has been demonstrated by harbor seals (Boness et al. 1994; Boness and Bowen 1996; Bowen et al. 2001) and ringed seals (Hammill et al. 1991; Kelly and Wartzok 1996), with a similar strategy thought to occur in other small phocids (Schulz and Bowen 2004). Caspian and other seals in the genus *Pusa* are the smallest extant seal species. By contrast, the large-bodied female gray seal does not forage during lactation (Boness and Bowen 1996; Boyd 2000), whereas female harp seals, of intermediate body size, have a strategy of foraging more and nursing less as their pups develop (Lydersen and Kovacs 1993), spending as little as 15% of their time with the pup just before weaning (Kovacs 1987a; Stewart 1987). In the present study, the overall frequency of stage 1–2 pups seen without their mother in attendance (38.9%) suggests that Caspian seal mothers may leave their pups to forage even when they are very young. During late season, however, the proportion of LPs (60%) was almost twice as high among stage 3–4 pups compared to stage 1–2, which could suggest a decreasing trend in maternal attendance towards late lactation as mothers spend more time foraging. The overall proportion of LPs (41%) recorded from the vessels was at the higher end of the range (9–48%, average 29%) observed during aerial surveys (2005–2012) of the breeding population on the ice in mid- to late season (Dmitrieva et al. 2015). It is likely that vessel disturbance contributed to this relatively high overall proportion of LPs seen along vessel corridors. Quiescence in LPs while mothers forage is thought to be normal, whereas restless and disorientated behavior may be a consequence of shipping disturbance. LPs in late season were not seen to aggregate or approach one another. A similar lack of gregariousness has also been noted for weanling harp and gray seals (Kovacs 1987a, 1987b).

Adult breeding behavior.—Single males were not observed to consort with a single female and her pup during early and mid-lactation, as occurs in spotted seals (Rugh et al. 1997) and gray seals on pack ice (Lavigne and Kovacs 1988). Observations in late season suggested that mating may occur in either of 2 scenarios. The first occurs when a single male approaches a female and pup, remaining close by them, often in the water. The second is when a male may occupy a position away from the pupping area where a female with no accompanying pup may join him on the ice or in the water. This mode of pairing would allow for a male to mate with more than 1 female in the same season and differs from harp seals, in which males circulate through nursery areas in late lactation and pursue multiple females across the ice (Lavigne and Kovacs 1988). Mating was not observed on the ice during this study, suggesting that it occurs in the water, as in harp and spotted seals (Merdsoy et al. 1978; Beier and Wartzok 1979).

No agonistic behavior between Caspian seals, thought to be males, was observed during the breeding season. Competition between adult male mammals for breeding is usually associated with sexual dimorphism, or having other secondary sexual characteristics (Ralls 1977). During the breeding season, the facial skin of male ringed and Baikal seals (*P. sibirica*) turns dark with sebaceous and apocrine glands producing a strong and characteristic scent (Ryg et al. 1992; Amano et al. 2000). During the breeding season, males deposit scent around access holes used by females. Beneath the scent-marked holes, the breeding males maintain territories that may include the lairs of several females (Smith and Hammill 1991). Distinct facial skin glands are lacking in male Caspian seals and conflict at access holes was not observed. Mature male Baikal seals are slightly larger than females (Amano et al. 2000), whereas both sexes are the same size in Arctic ringed seals (Krafft et al. 2006) and Caspian seals (Wilson et al. 2014). There are no obvious secondary sexual characteristics in male Caspian seals, suggesting that agonistic behavior among males during the breeding season is not likely (Ralls 1977).

The observations of Caspian seals during the breeding season reported here were limited and biased by the moving observation platform. Nevertheless, this is the 1st extensive description of pupping habitat, mother–pup behavior, pup development, and adult pairing behavior for this poorly known species. The traits that combine to form an overall reproductive system unique to Caspian seals include: 1) a small (5 kg) lanugal pup born on the ice surface, 2) an estimated lactation period of 3–4 weeks, 3) MPs in close proximity to one another (a few meters) with mutual tolerance, 4) use of deformed ice to shelter pups, although some pups are also born on flat ice without shelter, 5) strong avoidance of water by lanugal pups, and 6) male–female pairing in the water, without overt intermale agonistic behavior on the ice surface. Characteristics shared with other Holarctic small-bodied phocids include the pup's following response, the mother's chaperoning behavior, and the mother leaving her dependent pup to forage. This combination of behavioral traits is an adaptation to the winter ice conditions specific to the Caspian Sea.

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transits in late season of that year enabled observations of LAs during the presumed mating season. Twenty-two single LAs were recorded at polynyas, 8 in the water and 14 hauled out on the polynya edge. Four adult pairs were also seen at polynyas, 2 hauled out together at the edge and 2 swimming together in the water. On 1 occasion, 2 seals surfaced together very near the icebreaker, apparently having been surprised by it.

Discussion

Pupping habitat and group size.—The pupping habitat of Caspian seals is either land-fast ice with cracks or leads or stable drift ice, overlying water 3–5 m deep. Our observations suggested that ice-rubble fields are preferred over flat ice sheets as pupping habitat. The structure of the birth and nursery sites observed resembles that of harp seals, where small groups of mothers share access holes, often near ice ridges or other features that provide some shelter for pups (Lavigne and Kovacs 1988). The pupping habitat of Caspian seals also resembles the pre-lair habitat of Arctic ringed seals before sufficient snow has accumulated for lair construction, comprising ice-slab piles or pressure ridges with adjacent access holes (Smith and Stirling 1975). Some female Caspian seals pup in natural cavities in the pressure ridges, similar to a secondary type of birth lair of ringed seals in the Canadian Arctic (McLaren 1958). The more usual subnivean lairs of Arctic ringed seals require 20–150 cm of snow drifted over an access hole near the lee of a pressure ridge for a lair to be excavated (Smith and Stirling 1975)—conditions rarely achieved in the northern Caspian Sea.

Observations of adult seals in small groups on the ice, most thought to be pregnant females, suggest a degree of gregariousness among females about to give birth. This was further indicated by the typical minimum inter-neighbor distance between Caspian seal mothers of only about 2 m. This is less than for gray and harp seal mothers, which is at least 5–10 m (Lydersen and Kovacs 1999), and much less than for spotted seals (*Phoca largha*), which is characteristically 0.25–0.5 km (Rugh et al. 1997). The tolerance between neighboring mothers also is much greater for Caspian than for gray seals (Boness et al. 1982). A group of 2 or more Caspian seal mothers may share the area near a pile of ice slabs with access holes. This is in contrast to a complex of lairs in close proximity used by a single MP of Arctic ringed seals (Smith and Stirling 1975; Smith and Hammill 1991), with distances between lair complexes averaging 100–600 m (Kelly and Quakenbush 1990; Smith and Hammill 1991). For both Caspian and Arctic ringed seals, distance between birth sites may be influenced by the distances between suitable ice structures.

It has been suggested that the grouping of MPs of Caspian seals may have been influenced by predation pressure from eagles and wolves (Krylov 1990; Härkönen et al. 2008). During our study, eagles were sometimes seen feeding on pups although no attacks on live pups were witnessed. Wolf tracks were occasionally seen, and once were recorded beside a pup kill site. Caspian seal pups born on open ice would be more vulnerable to predation, particularly by eagles, than ringed seal pups inside snow lairs, and a group of Caspian seal mothers could possibly mount a more effective defense against 1 or 2 wolves than a lone mother. Unlike ringed seals, where the mother can move her pup underwater to another lair to escape predation from polar bears or foxes (Kelly and Quakenbush 1990), Caspian seal mothers have no such option. Although we often observed small groups of MPs near ice features, we also observed pupping areas where MPs were distributed about 2–10 m apart over areas extending to the limit of visibility from the vessel bridge. Wolves have been reported to kill up to 40% of pups on some breeding grounds (Krylov 1990). Until 100 years ago there were at least 10 times the present number of breeding seals (Härkönen et al. 2012) and also many more wolves. Historically, therefore, there may have been strong survival value in females pupping over a wide area, sufficiently close to each other to provide a "predator-swamping" advantage, but not so close as to elicit repeated kills of neighboring pups.

Thermoregulatory behavior of pups.—Caspian seal pups in lanugo actively avoided entering the water until late season when they were fat at stages 3 and 4. This water avoidance behavior has strong survival value because lanugo coats lose insulating properties when wet (Smith et al. 1991). For dry Arctic ringed seal pups, core body temperature can be maintained in air temperatures down to −25°C, but if pups are wetted, hypothermia may develop in air temperatures of −8 to −10°C (Smith et al. 1991). Ringed seal pups are sometimes forced to enter the water to escape predation by polar bears or foxes but are able to avoid irreversible hypothermia by returning to the lair, the temperature of which may be as much as 25°C higher than the outside air temperature (Smith et al. 1991). Caspian seal pups are the only seal species in which small lanugal pups of about 5 kg are typically born on open ice, often with minimal shelter from ice slabs or no shelter at all. Air temperatures in the northern Caspian Sea during the pupping season are typically −10 to −25°C, well below temperatures that could cause irreversible hypothermia for a wet pup. Water avoidance by young Caspian seal pups is therefore essential to survival. Even pups of species with greater birth weight, such as harp and gray seals, avoid water during the lanugal stage (Kovacs 1987a; Lydersen and Kovacs 1999).

Duration of the lactation period.—Our observations were insufficient to determine the precise length of the lactation period. The nursing period for all ice-breeding phocids is at least partly dependent on the degree of stability of their ice substrate. Gray and harp seals pup on relatively unstable ice floes and their lactation period is relatively short, at 15 and 12–13 days, respectively, whereas ringed seals breeding on more stable land-fast ice have a lactation period of 5–6 weeks (Lydersen and Kovacs 1999). The ice in the Caspian Sea is stable in most years at least to the end of the 1st week in March, 3–4 weeks after the peak of pupping at the end of the 1st week in February. Therefore, the nursing period for Caspian seal pups born in the last week of January or 1st week in February could be at least 4 weeks. Our late-season records show that 62% of all pups, including 37% of stage 4 pups (Supplementary Data SD3), were still attended by their mothers, suggesting lactation lasts at least 3–4 weeks. Therefore, a lactation period intermediate between gray and ringed seals but similar to spotted seals, which give birth on the pack-ice front (Rugh et al. 1997), is suggested.

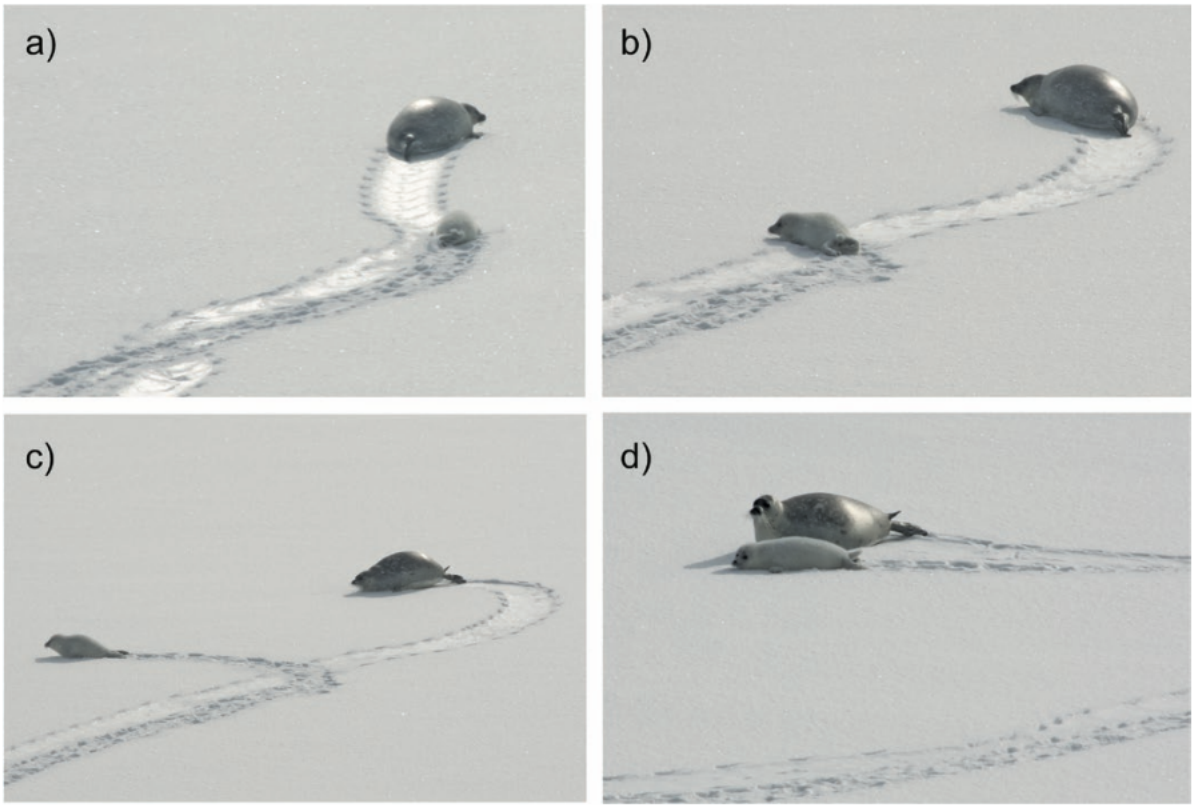

Fig. 6.—Time series of behavior of Caspian seals (*Pusa caspica*) showing: a) following behavior of a pup, b) pup stopping, c) pup turning around, and d) mother returning to pup after pup stops following.

(Supplementary Data SD4). Two exceptions were recorded in late February of 2010 and 2011. In 2010, 1 mother led her stage 2 pup away from the vessel into and across a polynya, and the pup followed in the water just behind her head. In 2011, a pup still in lanugo was recorded surfacing through an access hole. This was the only lanugal pup seen to have entered the water other than when disturbed by the vessel.

Lone pups undisturbed by the vessel usually appeared to be quiescent (Fig. 3d). Exceptions occurred (19 February 2010) in a breeding area that had been crossed by channels of several vessels. During 2 h of observation, 11 LPs were observed moving about in a disorientated manner. Five were distress-calling, 5 were partially wet from brash ice, 1 fell into a crack, and 2 were seen attempting to climb on to solid ice from brash ice. When an MP group was disturbed by the vessel, LPs would usually follow a neighboring MP (Fig. 7) or a neighboring LP. In the absence of a neighboring MP moving away from the vessel, LPs usually moved very little unless they were < 10 m from the side of the vessel. Late season LPs, i.e., near the age of weaning, showed little tendency to congregate: of 114 LPs and nearest neighbors recorded on 23 February 2011, 70% were separated by more than 10 m.

Single and paired adults during late season.—Observations of adult seals along the icebreaker route in late season suggested that adult male–female pairings may occur both near and away from the main pupping areas. During 16–23 February 2011, 24 occasions were photographed where an LA was close to an MP, either lying on the ice (n = 10) or surfacing through an access hole (n = 11) or polynya (n = 3). On 2 occasions where an LA surfaced through a hole, the mother went over to the hole and looked down it, and on 1 occasion went into the hole before returning to her pup. No defensive behavior was shown by the mother and no courtship activity was observed on the ice.

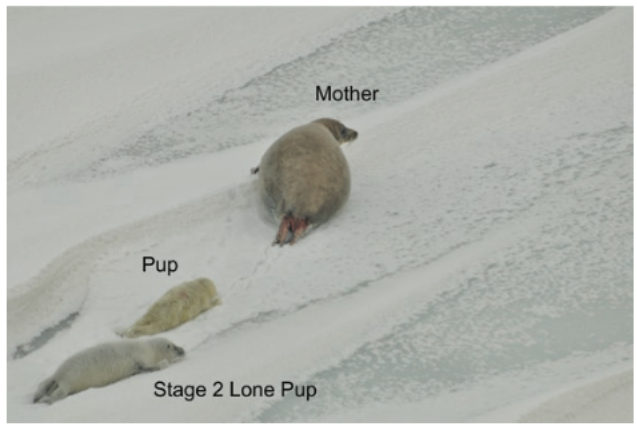

Fig. 7.—Mother Caspian seal (*Pusa caspica*) moving away from the vessel followed by her own (stage 1) pup and by a nearby (stage 2) lone pup.

Adult males during the breeding season can often be distinguished from females by their more slender pelvic region. On 25 February 2006, LAs, thought to be males, were seen along the vessel channel edge separated by ~10–20 m. These LAs were in the vicinity of MPs, but not close to them. Nine adult dyads were recorded in addition to 57 LAs on that transit. No bite wounds that might suggest agonistic behavior were seen.

In 2009, few pups were observed because the vessel route was tangential to the main seal-pupping areas. However,

abundance during the last week of February (Figs. 4c and 4d). Stage 2 pups were the most abundant developmental stage during February and over all the study period. Stage 3 pups were recorded from mid-February, with increasing frequency through late February. Stage 4 pups were seen only in late season, with the earliest observation on 20 February (Fig. 4). The relatively low counts of stage 3 and 4 pups compared to stage 2 suggests the peak abundances of stage 3 and 4 would be expected to occur from early March onwards and were not observed because our latest seasonal records of pup stages were made on 3 March.

The opportunistic nature of the observations limits our ability to assess variation in developmental stages among years in detail. However, a comparison of the proportion of pups by developmental stage on 25 February 2006 and 23 February 2011 (the best matched dates between 2 years with comparable sample sizes) found a significantly higher ratio of stage 1–2 pups to stage 3–4 pups in 2006 compared to 2011 (Table 4; odds ratio = 9.78; 95% confidence interval [*CI*] = 5.65–17.56; $P < 1 \times 10^{-15}$, Fisher exact test). This suggests that either peak pupping dates or rate of development varies from year to year.

Lone pups were frequently seen at nursery sites, often near an MP or another LP. Of 1,448 records of pups, 599 (41%) were LPs (Table 2; Supplementary Data SD3). Using data across all years, during late season, the relative occurrence of LPs among stage 3–4 pups was almost double that among stage 1–2 pups (59.8% of 189 stage 3–4 pups, 31.5% of 604 stage 1–2 pups; odds ratio = 3.2345; 95% *CI* = 2.279–4.610; $P < 6.5 \times 10^{-12}$, Fisher exact test), suggesting rates of maternal attendance may decrease for older pups.

Table 4.—Observed counts of developmental stages of pups of Caspian seals (*Pusa caspica*) in the northern Caspian Sea, from the photo records on 25 February 2006 and 23 February 2011.

Year	Pup stage				Ratio stage 1–2:3–4
	1	2	3	4	
2006	10	215	13	8	225:21 (10.71:1)
2011	0	98	50	40	98:90 (1.09:1)

Behavior of mothers and pups.—Although mothers and pups were typically observed resting close together on the ice surface, suckling was seldom recorded (6 times in 34 transits), probably due to disturbance caused by the passing vessel. However, on 19 February 2010, after the vessel had been stationary all night, 2 MPs close to each other (Fig. 3) were observed for 2.5 h after sunrise. A nursing bout began when a pup nudged the mother's side with its nose (Fig. 3a). The mother shifted position causing the pup to follow, then stopped and made nose contact with the pup (Fig. 3b). The pup then suckled for ~9 min (Fig. 3c). An hour later, the mother left the pup resting at the base of an ice ridge and moved directly and rapidly away, entering the water through an access hole beside an LP some 300 m distant. After she departed, the mother of the 2nd pair climbed on to a ridge behind the 2 pups and maintained an alert stance (Figs. 3d and 3e). When another LP approached her across the adjacent pan of ice, she approached, made nose-to-nose contact (Fig. 3f) and then returned to her position overlooking her own and her neighbor's pups.

When moving across the ice, mothers typically moved slowly while their pups followed closely behind. Mothers usually adjusted their pace to that of the pup, pausing or turning around to wait for it and making nose contact (Fig. 5). A pup would sometimes stop following if the mother got more than 5 m ahead and did not wait (Figs. 6a and 6b). This happened during close approach of a vessel, although mothers would usually return to their pups (Figs. 6c and 6d). Both mother and pup sometimes raised their tails while moving (Figs. 6c and 6d). A pup that lost contact with its mother would emit a "distress call" with open mouth and sometimes with raised head.

White-coat pups showed a marked aversion to entering the water by actively avoiding polynyas, access holes, and water-filled cracks, or they would remain on ice fragments

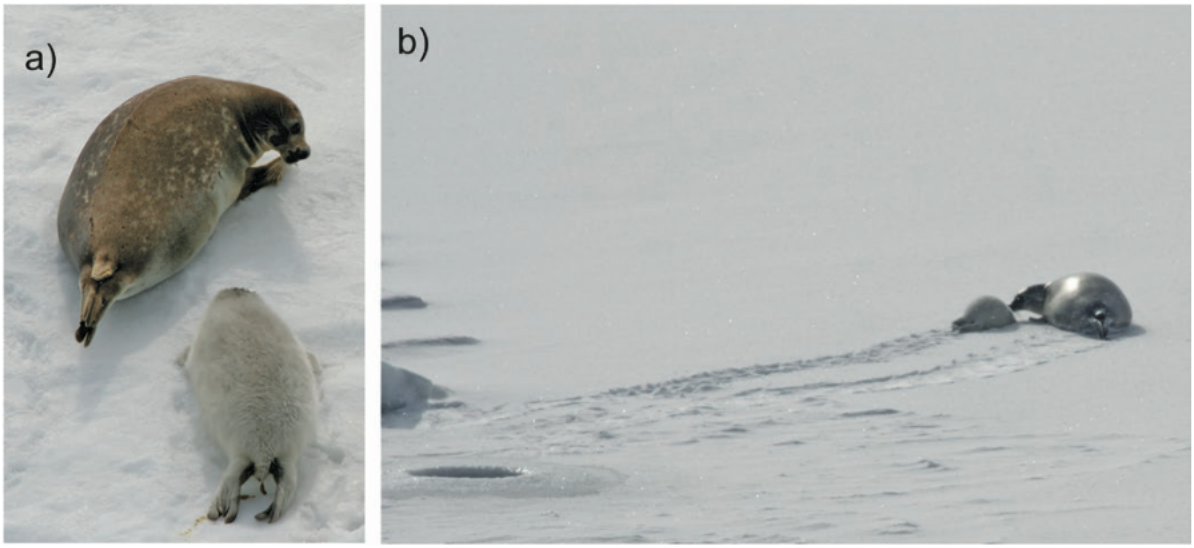

Fig. 5.—Photographs illustrating mother–pup movement behavior of Caspian seals (*Pusa caspica*): a) pup follows closely, mother turns to check pup and b) mother pauses and noses her pup.

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