**First paired observations of sexual behavior and calls in wild leopard seals**

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ABSTRACT

Little is known about the reproductive biology of the leopard seal (*Hydrurga leptonyx*), a Southern Ocean predator. Here we observed sexual behavior in wild leopard seals in Laguna San Rafael, Chile during a two-hour courtship interaction between a female and male. The female was hauled out on ice, mostly lying still (69% of the time) or moving (19%). The male was mostly under water (87%) or at the water's surface (11%). The female made seven in-air calls (i.e., thump-pulse, noseblast, blast, growl). The male produced 65 underwater calls (i.e., low and high double trills, unidentified trills). The underwater calls appeared to be directed toward the female. After the primary male vocalized for an hour, one or two unidentified leopard seals briefly swam near the female. After leaving the area, we heard underwater calls for another eight hours. The next day, the primary male was hauled out on ice with a swollen genital opening. The male was bleeding from a laceration caudal to the preputial opening, suggesting the male attempted to mate and that the female, or another seal, was responsible for the injury. Together, we find that leopard seal courtship involves a suite of behavioral and acoustic behaviors by both sexes, both in air and under water. This is the first description of leopard seal sexual behavior in the wild. Our study also provides the first evidence that leopard seals mate in South America.

# INTRODUCTION

Leopard seals (*Hydrurga leptonyx*) are generally solitary apex predators broadly distributed around the Southern Ocean (Hamilton 1939; Southwell et al. 2003; Forcada and Robinson 2006). Leopard seals spend much of their lives under water and live in remote, difficult-to-access locations (Hamilton 1939; Siniff 1991; Southwell et al. 2003). As a result, limited data exist for many aspects of their life cycle, including their reproductive biology.

Leopard seals have long been considered ice-obligate breeders that rely on Antarctic pack ice and floating ice for reproduction (Demaster et al. 1980; Siniff and Stone 1985; Southwell et al. 2003; Bester et al. 2021). A recent review showed that most of the 19 documented leopard seal newborn pups (84%) have been outside of Antarctica (e.g., subantarctic islands, Chile, New Zealand, Falkland Islands; van der Linde et al. 2022). From these 19 records, nine newborn pups were on ice, three were on land, two were in the water, and the remaining five were on unidentified substrates (van der Linde et al. 2022). Regardless of location, most pups were born between September and December, with a peak in November and December (Laws 1984; Laws 1993; Rogers 2018; van der Linde et al. 2022). Parturition is then followed by a potentially short lactation period (~10-14 days; Brown, 1957; Southwell et al. 2003; Kienle et al. 2022).

Mating is thought to occur 3-4 weeks after parturition, when the female is in estrus (Sinha and Erickson 1972; Siniff and Stone 1985; Rogers et al. 1996). Estrus has been documented in a single captive adult female leopard seal that had elevated estradiol levels in December coinciding with sexual receptivity (i.e., the female permitted mounting by a male; Rogers et al. 1996). Siniff and Stone (1985) suggested that the decrease in sightings of leopard seals on ice floes between November and December meant that the species mate under water. Weddell seals (*Leptonychotes weddellii*), the sister taxon to leopard seals (Fulton and Strobeck 2010), mates aquatically, with males attracting mates and defending underwater territories using vocal displays (Thomas and Stirling 1983; Thomas et al. 1983; Pahl et al. 1996; Harcourt et al. 2007). Therefore, leopard seal breeding season is thought to range from October to January, peaking between November and December (Southwell et al. 2003; van Opzeeland et al. 2010; Rogers 2017). However, to our knowledge, no one has documented sexual behavior (defined here as the actions and activities that animals engage in to find and attract mates and reproduce; Pfaus et al. 2001) in wild leopard seals. The only observations of copulation for the species came from a pair of captive leopard seals (November-February; Marlow 1967).

Acoustic behavior plays an important role in leopard seal communication, especially during the breeding season (Stirling and Siniff 1979; Rogers et al. 1995, 1996; Rogers and Cato 2002; Rogers 2007; Kreiss et al. 2013). Leopard seals have ~14 different call types (Rogers et al. 1995; Thomas and Golladay 1995; Rogers et al. 1996; Rogers and Cato 2002; Rogers 2007). Both sexes vocalize (Rogers et al. 1996), but most studies have focused on males (Rogers et al. 1995; Rogers 2007, 2014, 2017).

Research over the last 30 years has shown that male leopard seals exhibit individual, age, and geographic variation in underwater calls (Stirling and Siniff 1979; Rogers et al. 1995; Rogers and Cato 2002; Rogers 2007, 2014, 2017; Shabangu and Rogers 2021). Males produce loud and frequent underwater calls throughout the breeding season (Thomas and Demaster, 1982; Rogers

2007; Van Opzeeland et al. 2010; Kreiss et al. 2013; Rogers 2017). Calls peak between November and January, which potentially coincides with weaning and the female's estrus cycle (Thomas and Demaster 1982; Rogers and Cato 2002; Shabangu and Rogers 2021). The low and high double trill are the most common call types (Stirling and Siniff 1979; Rogers et al. 1995; Rogers 2014) and therefore thought to play a role in territorial behavior and attracting females during the breeding season (Thomas and Demaster 1982; Rogers et al. 1996). Rogers (2005), for example, describes male leopard seals as producing 'vocal courtship displays', where courtship is a reproductive communication system (often including vocal and behavioral displays) leading up to copulation (Morris 1956; Ewer 1968). However, it has been challenging to determine the function of different call types. As a result, call function has mainly been inferred from captive observations (Marlow 1967; Rogers et al. 1996) or from the timing of calls relative to the breeding season (Thomas and Demaster 1982; Rogers 2014; Shabangu and Rogers 2021).

In December 2022, we opportunistically observed leopard seal sexual behavior in Laguna San Rafael National Park, Chile. We collected acoustic and behavioral data from male and female leopard seals during a two-hour observation period. The next day, we observed one of the male leopard seals from the previous day hauled out on ice with physical indications of attempted copulation. To our knowledge, this is the first description of leopard seal courtship behavior in the wild. Our findings provide insight on the reproductive biology of this enigmatic Southern Ocean predator.

## METHODS

### *Data Collection*

We recorded behavioral and acoustic data from leopard seals during fieldwork in Parque Nacional Laguna San Rafael, Chile (46.62°S, 73.95°W). All work was done under Chilean permits SUBPESCA: R. EX. N° E-2022-717 and CONAF XI-21-2022 and approved by Baylor's Animal Care and Use Committee. We collected behavioral and acoustic data from a small boat from 18:10-20:16 on December 16, 2022 (hereafter, this two-hour interval is called the 'observation period'). We were 10-100 meters away from the seals throughout the observation period. Additional acoustic data was collected from our ship from 22:00 on December 16, 2022 to 6:30 on December 17, 2022. We also collected additional behavioral data from a small boat at 12:40 on December 17, 2022. Photos, videos, and acoustic data were recorded on multiple devices, including DSLR cameras, GoPros, and iPhones. When possible, the sex of each seal was visually confirmed.

### *Behavioral Data*

Video footage was analyzed and quantified in the open-access analysis software BORIS v. 7.13.9 (https://www.boris./unito.it/; Friard and Gamba 2016). We created an ethogram of point events (behaviors with no time duration) and state events (behaviors with a time duration; Table 1).

***Table 1**. Ethogram of point and state variables used to classify leopard seal behaviors from video footage during the observation period.*

| Location | Type | Behavior | Description |
|---|---|---|---|
| On ice | Point | Opens mouth | Seal opens its mouth |
| | Point | Closes mouth | Seal closes its mouth |

| | | | |
|---|---|---|---|
| | State | Mouth movements | Time from when seal first opens its mouth until it completely closes its mouth |
| | Point | Throat movements | Seal moves its throat in a vibrating or pulsate motion; often associated with producing sounds |
| | Point | Lifts head | Seal lifts its head off the ice |
| | Point | Lowers head | Seal lowers its head onto the ice |
| | Point | Swinging head | Seal swings its head from side-to-side |
| | State | Head movements | Time from when seal starts moving its head until it rests its head on ice; includes swinging, lifting, and lowering the head |
| | State | Foreflippers movements | Time from when seal starts moving its foreflippers until it rests foreflippers on ice |
| | State | Hindflippers movements | Time from when seal starts moving its hindflippers until it rests hindflippers on ice |
| | Point | Rolling | Seal moves body from side to side |
| | Point | Turning | Seal turns its body, moving to a new position |
| | State | Whole body movements | Entire body moves and/or shakes; this includes rolling, turning, and pulsate motions where the entire throat, neck, and chest vibrate |
| | State | Moving on ice | Time from when seal starts to move to when seal is lying still on the ice; this includes mouth, head, foreflipper, hindflipper, and whole body movements |
| | State | Lying on ice | Time from when seal is lying still on ice until seal starts moving any part of its body |
| | State | Not visible on ice | Time from when seal is not visible on ice until seal is visible again |
| In water | Point | Surfacing | Part of the seal's body rises above the water; multiple body parts may be out of the water simultaneously |
| | Point | Breathing | Seal makes audible inhale or exhale; sometimes accompanied by water droplets expelled from the nostrils |
| | Point | Spyhopping* | Seal raises its head vertically out of water and then sinks below the surface without much splash; the top of the seal's head can be angled 0-90° from the water's surface |
| | Point | Hauling out* | Seal moves its body out of the water by crawling or leaping onto land or ice |
| | State | Swimming | Time from when seal is above the water's surface and moving in a forward direction until it stops moving or is completely under water |
| | Point | Diving | A series of events starting with a seal lifting its head vertically out of the water with the body traveling forward; then the seal's head goes under water, followed by its highly arched back; finally, |

| | | | |
|---|---|---|---|
| | | | the hindflippers rise out of the water before sinking below the water |
| | Point | Under water | The seal’s body is submerged entirely below the water |
| | State | Not visible under water | Time from when seal is entirely under water to when the seal’s body (often the head and/or back) breaks the water's surface |
| Calls | State | In-air call | Time from first to last in-air call |
| | State | Underwater call | Time from first to last underwater call |

*Definition based on Würsig et al. (2018)

Behaviors were assigned to adult female LSR 07, adult male LSR 06, unidentified seal sighting 1, and unidentified seal sighting 2. Leopard seal identification numbers, residency status (i.e., whether the seal had been seen in previous months/years in Laguna San Rafael), and age class were obtained from a photo-ID catalog created by the Corporación Nacional Forestal (CONAF 2021, unpublished data). Leopard seals have unique pelage patterns and scars that can be used for photo identification (Forcada and Robinson 2006; Hupman et al. 2019; Grabham et al. 2024). To identify individual seals, we manually compared photographs of seals from this study with a reference catalog of known leopard seal individuals from Laguna San Rafael to determine matches (CONAF 2021 unpublished data). We recorded the time at which each behavior occurred and calculated the duration for all state events. For the video analysis, we focused on the relative amount of time each individual seal spent engaged in each behavior while video was recorded. We then calculated summary statistics for each state event.

### *Acoustic Data*

We isolated each leopard seal sound from the video recordings using the software Raven Pro 1.6 (Charif et al. 2010; https://ravensoundsoftware.com/). To assign calls to individual seals, we used the following criteria. For in-air calls, we identified the caller by the presence of a seal above the water when a sound was heard, as well as associated visual behavioral cues (e.g., head, mouth, and body movements) from video recordings., For the underwater calls, we followed the approach outlined by Rogers and Cato (2002), Rogers (2007), and Rogers (2017); specifically, the calling seal was identified if: (1) no other leopard seal calls were heard in the area at the same time, (2) calls began within five minutes of the identified seal diving under water, and (3) if calls were heard when the identified seal was under water and stopped when the identified seal was at the surface. Each call was analyzed for the following metrics: total duration (s), number of parts of the call, and duration of each part of the call (s). Based on the call characteristics, we assigned each one to a known leopard seal call type when possible based on previous work (Rogers et al. 1995, 1996). We calculated summary statistics for the acoustic variables.

## RESULTS

### *Behavioral Observations*

On December 16, 2022 at 18:10, we observed a leopard seal hauled-out on ice. The seal was visually confirmed to be LSR 07, an adult female and annual resident at Laguna San Rafael (first documented in 2012; CONAF 2021 unpublished data). As we approached within ~10 m, female

LSR 07 had her right lateral side on the ice with her back to the boat (Fig. 1a). Female LSR 07 remained hauled out on this ice floe the entire observation period.

We immediately observed another leopard seal swimming around the female's ice floe (Fig. 1b). This second seal was visually confirmed to be LSR 06, an adult male and annual resident at Laguna San Rafael (first documented in 2012; CONAF 2021 unpublished data). As we approached, male LSR 06 swam around the female's ice floe and spyhopped, lifting his head and neck above the water to look at female LSR 07 and toward the boat (Fig. 1b; Supplemental Movie 1). Then he dove and surfaced next to the female's ice floe twice. Throughout the observation period, diving was characterized by: (1) exhaling, (2) the top of the head rising vertically out of the water with the seal's body traveling forward, (3) the head going under water followed by its highly arched back, (5) the hindflippers coming out of the water, and (6) the hindflippers sinking underneath the water's surface (Supplemental Movie 1). On male LSR 06's next dive at 18:18, he vocalized twice under water, and this was the first call heard during the observation period (Supplemental Movie 1). All underwater calls were identified as low double trills, high double trills, or unidentified trills (Rogers et al. 1995). The underwater calls were loud, even above the water. After the first two calls, male LSR 06 dove and surfaced six more times. At the surface, male LSR swam alongside the female's ice floe, often lifting his head to look toward the female and sometimes toward the boat.

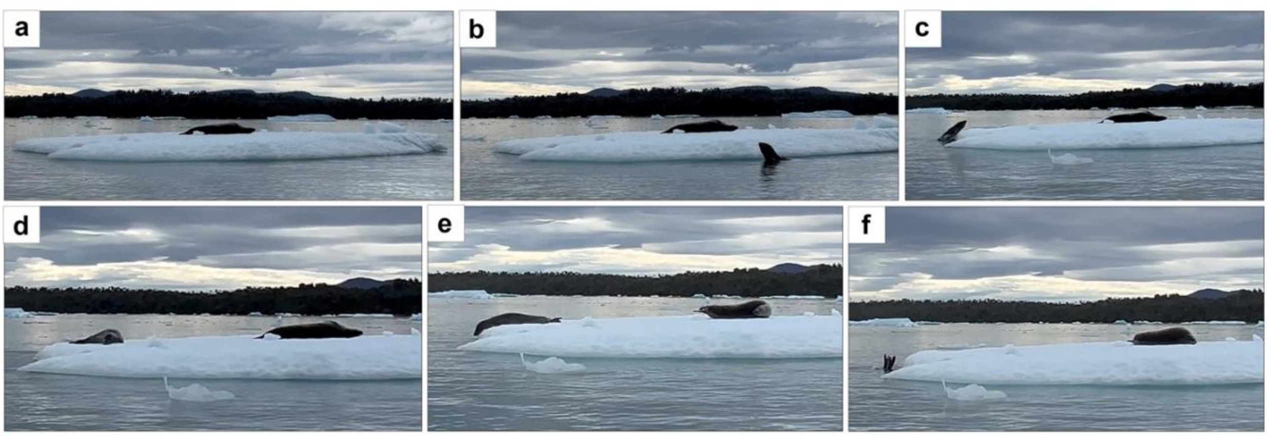


***Fig. 1*** *Interaction between adult female leopard seal LSR 07 and male leopard seal LSR 06. (a) Female LSR 07 lying on ice at the start of the observation period; (b) Male LSR 06 in the water spyhopping by female LSR 07's ice floe at the start of the observation period; (c) Male LSR 06 jumping out of the water; (d) Female LSR 07 and male LSR 06 hauled out; (e) Female LSR 07 swinging her head to look at male LSR 06; (f) Male LSR 06 diving into the water while female LSR 07 is watching. Photos by Emily Sperou*

Female LSR 07 alternated between lying still and moving (Supplemental Movie 1). Moving included: (1) lifting, lowering, and swinging the head from side to side, (2) opening and closing the mouth, (3) raising and lowering the foreflippers and scratching, (4) raising and lowering the hindflippers and shaking them), and (5) rolling and turning. Some of the female's movements overlapped with male LSR 06 calling under water, but some occurred while he was at the surface or not calling under water.

At 18:25, male LSR 06 dove, called under water twice, and then hauled out on the ice floe with the female (Fig. 1c-d; Supplemental Movie 1). LSR 06 did not approach the female, and she did not initially react to his presence (Fig. 1c-d). On the ice, male LSR 06 was in the same plane as the female, with his head facing both the boat and angled toward the female's hindflippers. Male LSR 06 was constantly moving on the ice; he rolled, turned his head and body toward the female, and then repositioned so that his head was along the ice edge (the opposite direction of the female; Fig. 1e). Female LSR 07 raised her head off the ice 45 s after the male hauled out and then swung her head to look at the male before lying back down (Fig. 1e-f). Twenty-two seconds later at 18:26, male LSR 06 dove back into the water, and the female watched (Fig. 1e-f). Male LSR 06 stayed near the female's ice floe, repeatedly surfacing alongside the ice floe. The male dove under water at 18:28.

Between 18:28 and 18:29, while the male was under water, female LSR 07 made three in-air sounds (Supplemental Movie 1**)**. During the first call, she raised her hindflippers and opened her mouth, producing a blast (Rogers et al. 1995, 1996) with her mouth open and starting to close. Then, she laid on the ice. Seven seconds later, female LSR 07 produced a second sound, noseblast (Rogers et al. 1995, 1996) while lying on the ice with her mouth closed and no body movements. An additional thirty-two seconds later, the female moved her hindflippers, raised her head off the ice with her mouth closed, and produced a third call, another noseblast. During the production of these in-air sounds, the male was not at the surface or vocalizing. The male surfaced 44 seconds after the second noseblast.

For the next ~70 minutes (18:29-19:36), male LSR 06 followed a repeated pattern: surfacing next to the female's ice floe, breathing, diving, making 1-8 underwater calls, and then surfacing again (Supplemental Movie 1). Underwater calls were only heard after male LSR 06 dove under water and never heard when he was at the surface.

At 18:39, male LSR 06 surfaced near the female's ice floe. After the male began a dive, female LSR 07 growled (Rogers et al. 1995, 1996; Supplemental Movie 1). When growling, the female was lying on the ice, her mouth was not visible, and she did not raise her head off the ice. Afterwards, female LSR 07 did not vocalize again for 87 minutes. For the next ~60 minutes (18:39 to 19:36), the female alternated between lying still and moving. Some of female LSR 07's on-ice movements overlapped with male LSR 06 vocalizing under water, but movements also occurred when LSR 06 was swimming at the surface and/or not vocalizing under water.

At 19:17, a leopard seal was observed at the water's surface at the edge of a nearby ice floe (hereafter, 'unidentified seal sighting 1'; Supplemental Movie 1). We could not get a clear view of this seal, so we could not visually match it with the CONAF photo ID catalog nor confirm it was not male LSR 06. This unidentified seal dove shortly after we first saw it. It surfaced again at 19:20, swimming toward female LSR 07's ice floe. The unidentified seal spyhopped with its head and neck out of the water (Fig. 2a) before diving under water or swimming out of sight behind female LSR 07's ice floe. The unidentified seal was observed a third time at 19:21 at the opposite side of female LSR 07's ice floe, swimming away from the ice floe before diving. While the unidentified seal was in the area, we recorded three underwater calls. The first call was at 19:18, while the unidentified seal was breathing at the water's surface. The second call was at 19:19, while the unidentified seal was spyhopping at the surface. The third call was at 19:20, after the unidentified seal was not visible behind the ice floe/under water. Because two underwater calls overlapped with the unidentified seal at the surface, we are confident that there were two seals in the water. However, since we did not see male LSR 06 immediately prior to the start of this bout of calls, we did not attribute these three calls to a particular seal. At 19:27, male LSR 06 surfaced near female LSR 07, dove, and began calling under water again.

Male LSR 06 was last seen diving by female LSR 07's ice floe at 19:36. Between 20:01 and 20:03, eight additional underwater calls were recorded. The calls were similar in type and duration to the previous calls made by male LSR 06. However, since we did not see male LSR 06 immediately prior to the start of this bout of calls, we did not attribute these eight calls to a particular seal. After these eight calls, no other underwater calls were recorded during the observation period.

At 20:03, another leopard seal (hereafter 'unidentified seal sighting 2') swam away from female LSR 07's ice floe (Fig. 2b; Supplemental Movie 1). We only saw the right side of this unidentified seal's head (for photo identification, we make individual matches from multiple views). The seal was potentially LSR 05, an adult male and annual resident at Laguna San Rafael first recorded in 2009 (CONAF 2021 unpublished data). However, with only one view of the seal's head, we cannot confirm that this seal was not male LSR 06 or the same unidentified seal from earlier. During the ~30 seconds that the unidentified seal was visible, it swam away from female LSR 07's ice floe until we could no longer see it behind ice floes or under water. No underwater calls were heard while this unidentified seal was in the area.

At 20:06, female LSR 07 produced three in-air sounds (Supplemental Movie 1). No other leopard seals were observed nearby or were calling under water. The three calls were all thump-pulses (Rogers et al. 1995, 1996). During the first thump-pulse, female LSR 07 was lying with her right lateral side against the ice and her ventral side toward us. The video was not in focus, but the sound was audible. A few seconds later, female LSR 07 made a second thump-pulse. During the call, female LSR 07 opened her mouth and slightly lifted her head dorsally from the ice. Her throat, neck, chest, and lower body vibrated side to side in time with the thumps. The female then lowered her head to the ice and breathed. The third thump-pulse call started eight seconds later characterized by the same behavioral pattern. After the third thump-pulse, female LSR 07 closed her mouth and laid on the ice. The female did not make any other sounds the rest of the observation period. We left the area by boat at 20:16 as it was getting dark (sunset was at 20:43). As we departed, female LSR 07 remained hauled out. We also saw a leopard seal swimming in the area as we departed, but we were unable to identify the seal.

Throughout the night (22:00) and into the next morning (6:30 on December 17; sunrise was at 6:14), we heard low and high double trill calls from our ship that was anchored 9-10 km from where female LSR 07 had been hauled-out on ice. The pattern and duration of the calls were like those produced by male LSR 06 during the observation period.

The following day, December 17, 2022 ~12:40, we observed male LSR 06 hauled out on an ice floe. No other leopard seals were observed or heard in the area. Male LSR 06 was lying with his

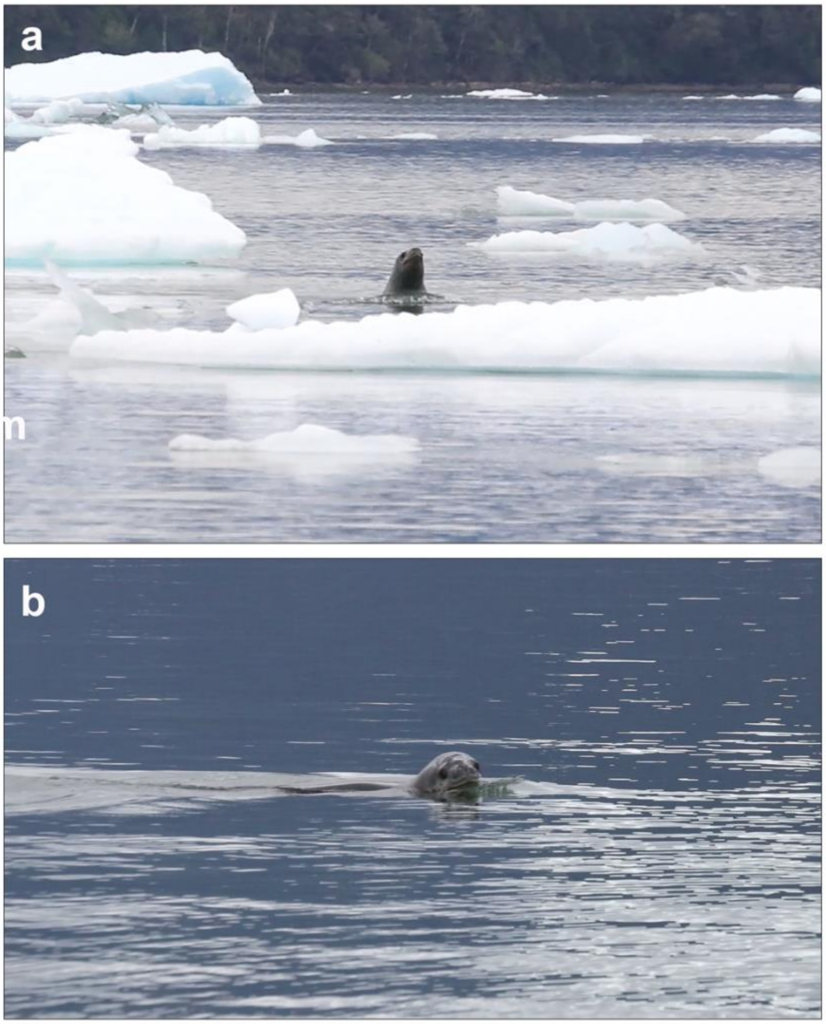


***Fig. 2*** *Two leopard seals sightings in the area during the interaction between female LSR 07 and male LSR 06. (a) Unidentified seal of unknown sex swimming by female LSR 07's ice floe; (b) Unidentified seal of unknown sex swimming away from female LSR 07's ice floe. Photos by Renato Borras-Chavez*

right lateral side on the ice. He was bleeding from an open laceration slightly right of the ventral midline and immediately caudal to the preputial opening (for the penis; Fig. 3a-b). Male LSR 06 had an enlarged and swollen genital area, especially the soft tissue surrounding the preputial opening. Part of the time we were by the ice floe, the tip of his penis was visible through the preputial opening (Fig. 3c).

*Behavioral Analyses*

We analyzed 68 minutes of video recordings from the observation period on December 16, 2022. We categorized 1,740 point and state events, which included in-air behaviors, in-water behaviors, and calls, for female LSR 07, male LSR 06, and unidentified seal sightings 1 and 2 (Table 2).

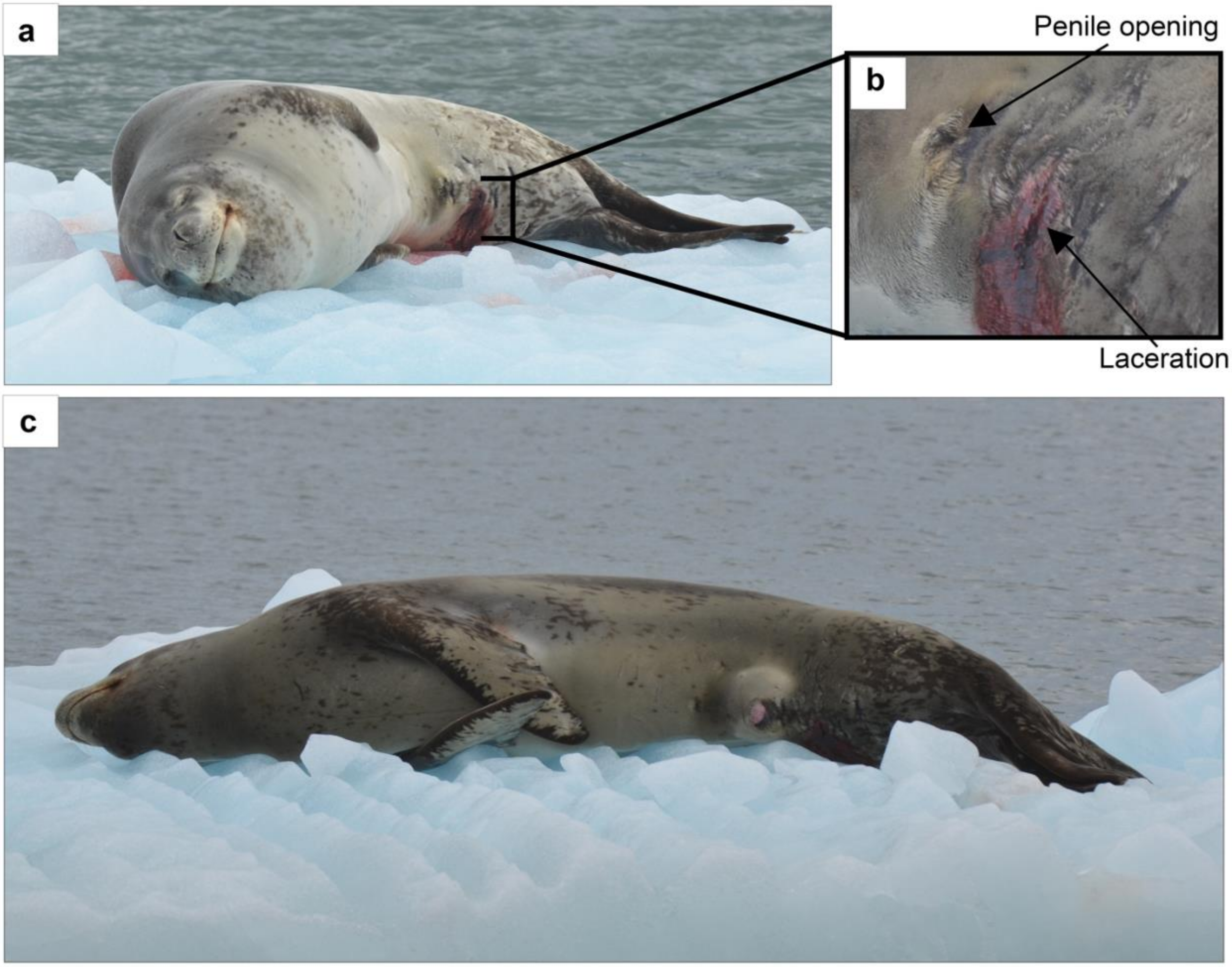


***Fig. 3*** *Male LSR 06 hauled out on ice on December 17, 2022, the day after courting female LSR 07. (a) Full body view of male lying on his right side with his ventral side visible; (b) Close up \ of the bleeding laceration caudal to the preputial opening; (c) Ventral view showing swollen tissue and penis visible by the preputial opening. Photos by Mike Goebel.*

Female LSR 07 spent most of the time lying still on the ice (n=153; 68.7% of time; Fig. 4). The periods where female LSR 07 was lying on ice lasted 19.1 ± 25.0 s (mean ± standard deviation). Female LSR 07 spent 19.4% of the time moving on ice, which included head movements (n=78; including throat movements, lifting, raising, turning, and swinging the head), mouth movements (n=58; including opening and closing the mouth), hindflipper movements (n=29), foreflipper movements (n=17), and whole-body movements (n=4; including shaking, rolling, and turning). Movements of different parts of the body often happened simultaneously. For example, when female LSR 07 lifted her head, she would frequently open her mouth and lift her hindflippers at the same time. These movements lasted 8.3 ± 6.8 s. Female LSR 07 was not visible in 11.9% of the videos (n=61); however, while not recorded in the video, we could see that female LSR 07 was either lying or moving on ice. We never observed female LSR 07 in the water.

In contrast, male LSR 06 spent most of the time under water (n=71; 87.4% of time), which lasted 49.7 ± 36.6 s (Fig. 4). Male LSR 06 spent 10.8% of the time doing surface behaviors (n=31; 10.8%). Surface behaviors included breathing (n=13), surfacing (n=54), spyhopping (n=4), swimming (n=31), and diving (n=28). These surface behaviors lasted 14.1 ± 10.6 s. Male LSR 06 also spent 1.8% of the observation period hauled out on ice next to female LSR 07, which included lying on ice (n=1; 1.0% of time; 41.0 s) and moving on ice (n=2; 0.8%; 15.6 ± 15.4 s).

During unidentified seal sighting 1, the seal was at the surface for 8.7% of the time it was observed and was known to be under water for 91.3% of its given observation period. During this time, the unidentified seal was surfacing (n=3), spyhopping (n=1), swimming (n=3), and diving (n=1). These surface behaviors lasted 4.9 ± 3.3 s. The first unidentified seal was last observed swimming away from the ice floe with female LSR 07 on it. During unidentified seal sighting 2, the seal was only observed at the surface for 28 s of the recorded observation period. During this time, the unidentified seal was surfacing (n=5), breathing (n=5), swimming (n=1), and diving (n=1). The second unidentified seal was last observed swimming away from the ice floe with female LSR 07 on it.

*Calls*

During the two-hour observation period, we recorded 84 calls (Table 3). These sounds included 54 low double trills (64.3% of sounds), 13 high double trills (15.5%), 8 unidentified trills (9.5%), 3 thump-pulses (3.6%), 2 noseblasts (2.4%), 1 blast (1.2%), 1 growl (1.2%), and 2 unidentified calls (2.4%; for representative spectrograms for these calls, refer to Rogers et al. 1995; Rogers et al. 1996, Rogers 2007; Kreiss et al. 2014; Rogers 2017; Shabangu and Rogers 2021). The first call was recorded at 18:18 and the last call during the observation period was at 20:06. Most calls occurred under water (89.3%), some were in air (8.3%), and the location (air or water) could not be determined for 2.4%.

Underwater calls only occurred when male LSR 06 was under water (Supplemental Movie 1). Most were produced when male LSR 06 was the only leopard seal observed in the area. We never heard multiple, overlapping underwater calls occurring the same time. Therefore, following Rogers and Cato (2002), Rogers (2007), and Rogers (2017), we assigned 65 of the 75 underwater calls to male LSR 06. Ten underwater calls occurred when no leopard seal was observed in the area, so these calls were not assigned to an individual.

Male LSR 06 spent 7.7% of the recorded observation period calling (Table 3). Most of male LSR 06's underwater calls were low double trills (73% of underwater calls). The low double trill had a duration of 5.2 ± 1.0 s and was characterized by two distinct segments; the first was 2.4 ± 0.5 s, and the second was 3.0 ± 0.5 s. The second most common underwater call was the high double trill (18% of underwater calls). The high double trill had a duration of 1.7 ± 0.4 s and two distinct parts; the first segment was 0.9 ± 0.2 s, and the second was 0.7 ± 0.2 s. Some underwater calls were categorized as unknown trills (9% of underwater calls). These unknown trills were acoustically like the high double trill but differed by not having two distinct parts. The unknown trills had a duration of 0.9 ± 0.3 s. It is possible that these unknown trills were either medium

***Table 2***. *Behavioral state data for the primary male and female leopard seal during the observation period.*

| Behavior | Female LSR 07 | | | Male LSR 06 | | |
|---|---|---|---|---|---|---|
| | N | Total Duration (s) | Mean Duration (s) | N | Total Duration (s) | Mean Duration (s) |
| Lying on ice | 153 | 2,773.7 | 19.1±25.0 | 1 | 41.0 | 41.0 |
| Moving on ice | 94 | 783.6 | 8.3±6.8 | 2 | 31.3 | 15.6±15.4 |
| Head | 78 | 522.0 | 6.7±5.1 | 3 | 17.3 | 5.8±5.5 |
| Mouth | 58 | 231.7 | 4.0±3.0 | 0 | 0.0 | 0.0 |
| Foreflippers | 17 | 71.0 | 4.2±2.4 | 0 | 0.0 | 0.0 |
| Hindflippers | 29 | 189.3 | 6.5±3.8 | 1 | 4.8 | 4.8 |
| Whole body | 4 | 11.0 | 2.7±0.7 | 4 | 17.0 | 4.3±1.6 |
| Not visible on ice | 61 | 481.3 | 7.9±11.4 | 0 | 0.0 | 0.0 |
| Surface behaviors | 0 | 0.0 | 0.0 | 31 | 436.6 | 14.1±10.6 |
| Under water | 0 | 0.0 | 0.0 | 71 | 3529.5 | 49.7±36.6 |
| Total Observation Duration (s) | 4,038.6 | | | 4,038.4 | | |

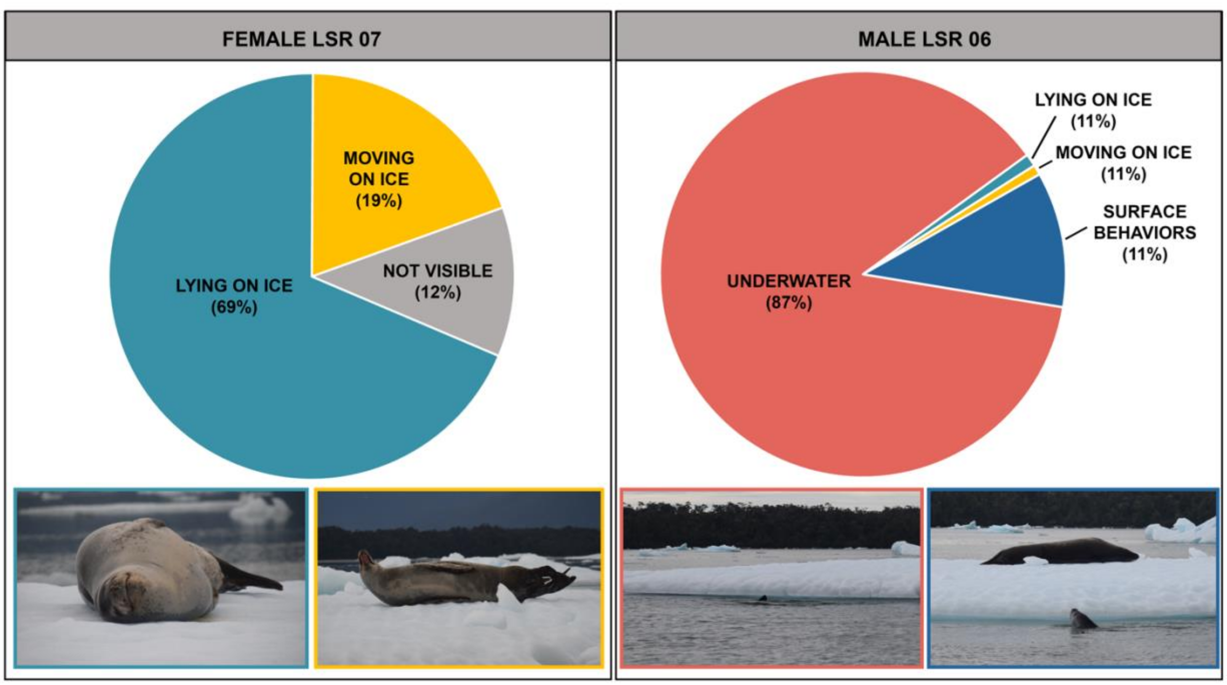


***Fig. 4*** *Proportion of time female LSR 07 and male LSR 06 spent in different behavioral states with representative photos (from left to right) of female LSR 07 lying on ice, female LSR 07 moving on ice, male LSR 06 diving under water (only tips of hindflippers visible), and male LSR 06 surface behaviors. Photos by Sarah Kienle*

*__Table 3__. Call types produced by the adult male and female leopard seal during the observation period, along with the number of calls and their mean duration (mean ± standard deviation).*

| Seal | Call Type | Number | Duration (s) |
|---|---|---|---|
| Male LSR 06 | Low double trill | 47 | 5.2 ± 1.0 |
| | High double trill | 12 | 1.7 ± 0.4 |
| | Unidentified trill | 6 | 0.9 ± 0.3 |
| | **TOTAL** | **65** | **312.8** |
| Female LSR 07 | Thump-pulse | 3 | 3.8 ± 0.4 |
| | Noseblast | 2 | 0.7 ± 0.3 |
| | Growl | 1 | 2.3 |
| | Blast | 1 | 0.6 |
| | **TOTAL** | **7** | **14.5** |

single trills (Rogers et al. 1995, 1996) or partial recordings of high double trills. Regardless, low double trills always occurred before either the high double trill or the unknown trill.

We recorded seven in-air calling, that included the thump pulse, noseblast, blast, and growl (Supplemental Movie 1). All in-air calls were produced by female LSR 07 on ice. Female LSR 07 spent 0.4% of the recorded observation time calling (Table 3). The most common in-air call was the thump-pulse (n=3; 42.9% of in-air calls). The thump-pulse was characterized by female LSR 07 lying on her side on the ice, opening and closing her mouth and slightly lifting the head dorsally, with her throat, neck, and chest vibrating in time with the call. The thump-pulse lasted 3.8 ± 0.4 s. The second most common in-air call was the noseblast (n=2; 28.6% of in-air call). The noseblast sounded like a sneeze. The female produced the first noseblast while lying on her side with her mouth closed and no associated movements, and the second one was associated with raising her head and lifting her head dorsally off the ice with her mouth closed. The noseblast lasted 0.7 ± 0.3 s. The blast (n=1; 14.3% of in-air calls) was characterized by the female lying on her side and opening her mouth. The blast lasted 0.6 s. The growl (n=1; 14.3% of in-air calls) was a moan-like, rumbling sound that lasted 2.3 s and was not associated with any head or body movements. All in-air calls by female LSR 07 were produced when she was alone on the ice floe.

## DISCUSSION

This is the first description of sexual behavior in wild leopard seals. We found that leopard seal sexual behavior involves a suite of behavioral and acoustic behaviors by both sexes. Our results demonstrate the importance of in-air and underwater calls during the breeding season (October – January), which corroborates previous studies on the species (e.g., Stirling and Siniff, 1979; Rogers et al. 1995; Van Opzeeland et al. 2010; Rogers 2007, 2014). Together, our data provide important insights on leopard seal reproductive biology.

The two sexes primarily operated in different mediums. The male was mostly under water, while the female was hauled out on ice the entire time. Likewise, the sexes vocalized in different mediums; the male only vocalized under water, while the female only vocalized in the air. Using ice for sexual behaviors is consistent with descriptions of the species as ice-obligate breeders (Demaster et al. 1980; Siniff and Stone 1985; Southwell et al. 2003; Bester et al. 2021).

Here, the adult male leopard seal made at least 65 underwater calls during repeated bouts of diving across the two-hour period. After we left the area, we continued to hear the same calls for another 8.5 hours that were potentially made by the same male (male LSR 06). Our results suggest that this one male spent at least two and potentially up to 12 hours vocalizing under water as part of courtship. Lone male leopard seals can vocalize under water for hours (Rogers 2007), especially during the breeding season (Thomas and Demaster, 1982; Rogers et al. 1996; Van Opzeeland et al. 2010). Several studies have shown that the frequency of low and high double trills made by males dramatically increases during the breeding season (Stirling and Siniff, 1979; Thomas and Demaster 1982; Rogers et al. 1995; Rogers and Cato 2002; van Opzeeland et al. 2010; Rogers 2007, 2014; Shabangu and Rogers 2021). Further, these two call types have been documented in every breeding leopard seal aggregation in the South Shetland Islands and around Antarctica (Stirling and Siniff, 1979; Rogers et al. 1995; Rogers 2007, 2014, 2017). Our study provides the first report of low and high double trills in leopard seals from South America, emphasizing how common these calls are across the species range.

The male produced the low double trill four times more frequently than the high double trill. Previous studies found geographic differences in the proportion of these two call types – from more low double trills in pack ice in the Davis Sea (Rogers 2014) to equal numbers of low and high double trills in Prydz Bay and the Davis Sea (Rogers and Cato 2002; Rogers 2007). However, previous studies noted that these patterns (and those presented here) may reflect differences in propagation and call source levels between the call types, rather than intraspecific variation in the type of calls (Rogers 2014).

Regardless of call type, male leopard seal underwater calls are loud (Stirling and Siniff 1979; Rogers 2014; this study), and these sounds are referred to as 'broadcast' calls (Rogers et al. 1995, 1996). Stirling and Siniff (1979), for example, described hearing leopard seal calls through the hull of their ship. Similarly, Rogers et al. (2014) heard underwater calls above the ice. Here, we heard leopard seal low and high double trills inside our ship >8 kilometers from where we had last seen leopard seals.

These loud underwater calls (especially low and high double trills) likely play a role in female mate choice and/or male competition/territorial displays (Rogers et al. 1996; Rogers and Cato 2002; Rogers 2007, 2017). Many aquatic mating pinnipeds use vocal courtship displays during their species' breeding season, from bearded seals (*Erignathus barbatus*) to walruses (*Odobenus rosmarus*; Ray and Watkins 1975; Stirling et al. 1987; Fay et al. 1984; Sjare and Stirling 1995; Van Parijs et al. 1999, 2001). In widely dispersed and solitary species like leopard seals, loud stereotyped underwater calls travel long distance and may help overcome the challenges of communicating and finding mates (Rogers 2017; Shabangu and Rogers 2021). The increase in leopard seal call frequency and rates during their breeding season suggests that these underwater calls are an important part of male mating behavior (Rogers and Cato 2002; Rogers 2017)., maintaining a repeated pattern of breath-holding and calling may function as an indicator of fitness (Rogers and Cato 2002; van Opzeeland et al. 2010; Rogers 2017). Larger male leopard seals, for example, produce more consistent, stable calls throughout the breeding season than smaller males, suggesting these calls showcase a male's breath-holding ability and stamina (Rogers 2017). However, it has been difficult to test the function of different call types in wild leopard seals because of the difficulties in recording behavioral and acoustic data from individuals of known age, sex, and body size.

The repeated underwater calls by the male leopard seal (LSR 06) appeared to be directed toward the lone female on ice. The male remained near the female for at least two hours, repeatedly calling near the female. The male frequently surfaced by the female's ice floe between bouts of diving. Further, we heard low and high double trills both when we were and were not in the area, showing that the production of these calls was not influenced by our presence. The loud underwater calls of the primary male (LSR 06) may also have garnered the attention of another nearby leopard seal(s) that then came over to investigate. However, it is also possible that the female's in-air calls brought these other leopard seals to the area. Broadly, these observational data suggest that the underwater calls by males are an important part of courtship, potentially used to attract the attention of specific females, while potentially also announcing the courtship attempt to others in the area (Rogers 2003).

Most studies on phocid (seal) mating have focused on male behavior and calls (e.g., bearded seals, Weddell seals, and harbor seals [*Phoca vitulina*]; van Parijs et al. 1997, 1999, 2001, 2006; Moors et al. 2004; Harcourt et al. 2007); this has also been true for leopard seals (Rogers et al. 1995; Rogers 2007, 2014, 2017). The focus on male calls is partly due to the widespread use of underwater hydrophones, automatically resulting in more data from the individuals (mostly males) that call under water. One of the only studies to document calls of a female leopard seal found that a captive female primarily called from the beginning of estrus until mating (Rogers et al. 1996). The authors suggested that female leopard seals may use acoustic displays to advertise their sexual receptivity over long distances to broadly dispersed males (Rogers et al. 1996; Rogers 2003). Similarly, our observations of the behavioral and acoustic displays of a wild female leopard seal suggest that females play more than a passive role in sexual behavior.

While the male leopard seal made more calls than the female, the female produced a greater variety of sound types, including noseblasts, thump-pulses, a blast and growl. Based on observations of a male and female leopard seal in captivity, the blast and growl are used during aggressive encounters between conspecifics, such as lunging and slapping (Rogers et al. 1996). Wild leopard seals also produce blast and growl calls in response to other species, including humans (Rogers et al. 1995). The noseblast has only been documented in captive leopard seals, where it was produced during both aggressive and defensive behaviors between a male and female (Rogers et al. 1996). Here, the female produced the blast and noseblasts right after the male (LSR 06) hauled out on the same ice floe. The thump-pulse call has also been used in both aggressive and defensive behaviors in both captive and wild interactions (Rogers et al. 1995, 1996). Further, the thump-pulse is distinguished as the only female call recorded during mounting/attempted mountings during the observations of captive leopard seals during the breeding season (Rogers et al. 1996). Here, the thump-pulse calls were produced a few minutes after the last underwater calls were heard during the observation period,. All in-air calls were made while the female was awake; some leopard seals have been documented making in-air calls while hauled out and sleeping (Stirling and Siniff 1979).

There are several possible explanations for why the female leopard seal made the different call types and what information was communicated. First, our mid-December observation overlaps with hypothesized estrus for female leopard seals. However, each female's estrus period depends on the timing of pupping and ovulation (Laws and Sinha 1993). The purpose of different calls likely differs depending on the timing of the estrus cycle (Rogers et al. 1996), and we do not know if this female was in estrus. Estrus has only been documented in a single captive female that had increased estradiol concentrations and showed behavioral sexual receptivity (i.e., permitted a male to mount her) in December (Rogers et al. 1996). Second, it is not clear whether leopard seals mate on ice or in water. Most polar pinnipeds, including other Antarctic phocids (i.e., crabeater, Ross, and Weddell seals), mate aquatically (Van Opzeeland et al. 2008, 2010). However, copulation has not been documented in wild leopard seals, and this species shows an unusual degree of female-biased sexual dimorphism that may influence their mating system (Hamilton 1939; Kienle et al. 2022; Sperou et al. 2023). Third, the calls and behaviors made by the female could suggest both interest or disinterest in mating. For example, if copulation occurs under water, the aggressive and/or defensive calls and the fact that the female remained hauled out on ice may have signaled disinterest. Alternatively, if mating occurs on ice, the thump-pulse calls and the fact that the female remained on ice may have signaled interest. Finally, the female may have produced these calls in response to our team's presence, especially toward the beginning of the observation period when our boat was closest to the female's ice floe. Leopard seals have made calls (e.g., the growl, blast, and thump-pulse) in response to human approach (Rogers et al. 1995); however, these calls have also all been used in intraspecific interactions (Rogers et al. 1996). Here, most of the female's calls were made when the female was not looking at us. Additionally, no leopard seals, including this female, vocalized in response to our presence at any other point during this same field work.

We did not observe any copulation attempts in this study. A recent study described the large baculum of a male leopard seal and suggested that their large baculum size is likely associated with a long intromission (Rule et al. 2023). The only observations of copulation for the species were between a captive male and female in shallow (~0.5 m) of water with copulation lasting ~10 minutes (Marlow 1967). During the of copulation, observers described that the male made 'gargling' calls below the water, and 'grunting' calls at the surface (Marlow 1967). On February 18, after copulating the day before, the female leopard seal was found dead with multiple severe lacerations the following day but cause of death could not be determined, although the male clearly played some part in her injuries (Marlow 1967).

The day after our observation of courtship, the male (LSR 06) was hauled out on ice with a bleeding cut immediately caudal to his preputial opening. In addition, his preputial opening and the region between the umbilicus and preputial opening were swollen. Marlow (1967) described a similarly large swelling at the base of the male's penis after an observed copulation between a captive male and female leopard seal. We suggest that the male attempted to mate with a female, and that either the female, or another leopard seal in the area, were the cause of the wound near his preputial opening.

Together, our study shows that leopard seal sexual behaviors occur in Laguna San Rafael. This finding aligns with previous reports of leopard seal pups in the lagoon (Boop 2014; van der Linde et al. 2022). Up to five pups have been documented in Laguna San Rafael from 2013 to

2022 (Boop 2014; van der Linde et al. 2022; CONAF, pers. comm.). In Chile, only two other leopard seal pups have ever been documented, both in Tierra del Fuego (2012 and 2015; Acevedo et al. 2017). Laguna San Rafael may therefore be an important breeding site for leopard seals outside of Antarctica. More broadly, these observations of sexual behavior and leopard seal pups in South America correspond with a recent review of sightings of leopard seal births and pups which showed most sightings of newborns and pups occurred outside Antarctica (van der Linde et al. 2022). These data provide additional evidence that leopard seals can—and are—breeding outside of Antarctic pack ice.

Our opportunistic observation of leopard seal sexual behavior in Laguna San Rafael offers new insights into the reproductive biology of this species. The present study was limited by a small sample size and short observation period. Additionally, we cannot rule out the possibility that the our presence at the site may have influenced some leopard seal behavior. Nevertheless, we provide the first documentation of sexual behavior in wild leopard seals. Future work will undoubtedly expand upon these findings, and we emphasize the need to collect paired in-air and underwater acoustic and video data of known sex individuals to better understand the role of competition, territoriality, and female choice in the mating behavior of leopard seals. Leopard seals are important Southern Ocean predators; understanding their reliance on sea ice and the drivers of reproductive success within and between populations is crucial for predicting how this species is—and will—respond to rapidly changing conditions across the southern hemisphere.

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AUTHOR CONTRIBUTION STATEMENT

SSK: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, visualization, writing (original draft, review & editing). CAB: Conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, writing (review & editing). GG: Funding acquisition, project administration, resources, writing (review & editing). MEG: Conceptualization, data curation, investigation, methodology, resources, writing (review & editing). MD: Investigation, methodology, resources, writing (review & editing). ESS: Conceptualization, data curation, funding acquisition, investigation, methodology, resources, visualization, writing (review & editing). AIG: Conceptualization, data curation, investigation, methodology, resources, writing (review & editing). RBC: Conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, writing (review & editing). All authors contributed to the article and approved the manuscript.

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