Social Interactions of Stranded and Recovering Immature California Sea Lions (*Zalophus californianus*)

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Abstract

Hundreds of California sea lions (*Zalophus californianus)* strand along the Pacific coast of North America each year. They are treated for a variety of conditions at marine mammal clinics along the coast, including malnutrition, physical trauma, infections, and toxicosis. The largest clinic is The Marine Mammal Center (TMMC) in the Marin County Headlands just north of San Francisco where sea lions can reside for weeks to months before release. Assessment of illness and recovery can be difficult. Since healthy sociality is sensitive to developmental impairment and illness, understanding of typical social interactions would aid in the assessment of overall recovery. To gain insight to the social behavior of captive California sea lions, we examined the behaviors of recovering immature individuals at TMMC. We found that the sea lions in male pens were generally more physically active, expressing more approach interactions and coordinated swimming per day. The sea lions in mixed-sex pens fluctuated in activity, with the level of activity decreasing as the day went on; while the sea lions in male pens maintained similar levels of activity all day. These findings offer a foundation for more rigorous studies of the social neurobiology of recovering California sea lions.

Key Words: California sea lions, social behavior, sociality, adolescence, swimming behaviors

Introduction

Marine mammals are often found stranded along the California coastline during late spring through early autumn (Greig et al., 2005). Predominantly pinnipeds, these individuals are retrieved from the coastline and brought to centers along the California coast where they are treated and released. The largest of these centers, The Marine Mammal Center (TMMC), is located in the Marin County Headlands, just north of San Francisco. Veterinarians and volunteers at TMMC treat pinnipeds for a variety of diseases, including infection with viral and bacterial pathogens, malnutrition, physical injury, and exposure to neurotoxins.

Strandings of California sea lions (*Zalophus californianus*) often exceed 100 individuals per year with occasional years marked by large spikes (Greig et al., 2005). Between 2002 and 2012, 5,660 sea lions were admitted to TMMC, of which 2,139 were released; 40 recovered but were placed in facilities; and 3,408 were either picked up as carcasses, died on arrival, or were euthanized. A total of 1,256 juveniles were treated at TMMC of which 714 died, 532 were released, eight were relocated, and two were placed in facilities. Malnourished juveniles totaled 188 individuals; and during our study period (July to November 2012), 25 of these malnourished individuals were treated at TMMC. In addition to malnourishment, sea lions come to TMMC with injuries from physical trauma; viral and bacterial pathogens (such as leptospirosis); high body burdens of anthropogenic compounds (such as PCBs and perfluorinated octane sulphonate); or exposure to domoic acid, a neurotoxin produced by algae, most commonly a species of *Pseudo-nitzchia* (Fryxell et al., 1997; Scholin et al., 2000).

Assessments of recovery can be difficult, especially with chronic conditions such as malnutrition or domoic acid exposure. Many individuals are diagnosed with multiple conditions and experience additional stress from medications, human interactions, and the confinements of recovering in captivity. In light of the many factors that contribute to disease and stress in marine mammals, refinements in our assessments of sea lion health are necessary

to improve diagnostic and treatment outcomes. Social interactions are highly sensitive to physiological and psychological injury such as malnutrition (Almeida & De Araujo, 2001). Behavioral assessments of social ability could help us determine if and when a given sea lion is responding to treatment or is ready for release.

Despite the obvious potential value of assessments of social behavior, little is known about the behaviors of sea lions recovering in pens. Observation of sea lion social behavior inside recovery pens has not been reported, so we lack knowledge about the range of social behaviors expressed by captive individuals as well as variations among male and female sea lions or juveniles and adults. Without understanding of diel rhythms of social interaction, we lack even basic understanding of when to observe sea lions and what behaviors to expect from immature males and females. To adequately assess sea lion social behavior at any point during their treatment, we need to be able to observe them for short periods during specific times of the day and use the collected data to develop informed plans for sea lion treatment and release.

The current study was designed to gain basic understanding of the social behaviors of California sea lions in their recovery pens, determine the time of day we might optimally observe sea lion social behavior, and develop preliminary ethograms that help us classify social behaviors so we can compare sea lions expressing different levels of social functioning. To achieve these goals, we took advantage of a stranding event between July and November of 2012 to examine patterns of sea lion social behaviors. We observed immature sea lions that were weaned but not yet reproducing. Sea lions were housed in pairs and observed by remote video capture as they recovered in outdoor pens.

Methods

Between August and November of 2012, captive immature California sea lions (11 males and 4 females) were observed at TMMC inside pens measuring 6.1 × 4.6 m and containing central pools of 2.5 × 2.5 × 1.4 m, filled to a depth of 1.1 m. Stranded individuals were assessed for age (females between the ages of 1 and 5 y old and males between the ages of 1 and 8 y old, classified as yearlings, juveniles, or subadults) and health condition. Staff at TMMC estimated age based on a variety of factors, including, but not limited to, sex, sexual dimorphism, standard length, physical presentation of flippers, head and teeth development, and natural history knowledge of time of year. Recovering sea lions were assigned to our observation pens to accommodate their shared nutritional requirements.

Treatment protocols determined whether an individual was fed four times daily (0800, 1200, 1600, and 2200 h) or three times daily (0800, 1400, and 2000 h). Pens that contained two to seven individuals that were fed three times daily were video recorded via surveillance IP cameras (M12D, Mobotix Corp., Winnweiler, Germany). We report herein an analysis of pens containing two sea lions.

Sea lion movement triggered IP cameras to video record their behaviors. Camera settings were designed to include all sea lion movements during visible hours of the day and to exclude other movements, such as wave activity, within the pens. Five zones were selected in the pen, including rectangular zones capturing activity along each side of the pool, between the pool wall and the fence around the pen, and a zone capturing swimming activity inside the pool (Figure 1). IP cameras were triggered to record when 13% of the pixels changed color within any of these five zones. Sensitivity for individual pixels was set for 0% so that any detected change in wavelength contributed to the possibility of a recording. Once triggered, recordings were retroactively stored for the 2 s before the trigger and continued for 2 min, ending after the last motion detected within the camera's field of view.

Audio-video recordings were stored on IP cameras utilizing the Mobotix MxPEG codec at 25 frames/s with 800 × 600 pixel resolution. Data retrieval from IP cameras to remote computers was conducted midday when investigators were more reliably able to download videos from the remote cameras. When video recordings exceeded the memory capacity of IP cameras, the oldest videos were overwritten to accommodate the most recent recordings. As a result, recordings of sea lion behaviors collected during the morning hours may have been overrepresented in our dataset. We collected approximately 29 recorded hours of AM activity and 16½ recorded hours of PM activity.

Individual sea lions were tracked with a colored, 12.7-cm wide grease mark (All-Weather Paintstik, La-Co Industries, Inc., Elk Grove Village, IL, USA) drawn along the sagittal plane between the shoulder blades to midway down the backbone. Sea lions were grease marked each week to ensure on-camera visibility. We could also identify individual sea lions from their flipper tags and from obvious differences in length, girth, coloring, various malformations, injuries, and variations in flipper shape. A spreadsheet maintained by TMMC staff contained identification and treatment information about each animal. This information is presented in Table 1.

Recordings were edited to exclude footage triggered by human activity inside the pen (e.g., feeding and cleaning) and physical movements unrelated to sea lion activity (e.g., wavelets inside the pools).
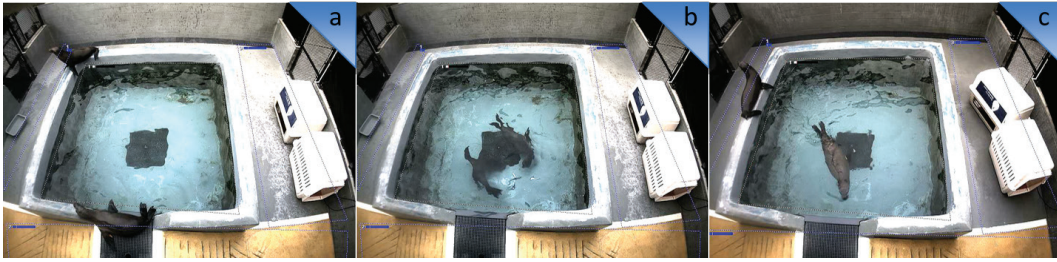
Figure 1. California sea lion (*Zalophus californianus*) pens at The Marine Mammal Center (TMMC). Active sea lions expressed a variety of social and nonsocial behaviors. Within a single pen, #10357 and #10361 engage in both social and nonsocial behaviors. Figure 1a shows a single frame of both sea lions on land but not socially engaged; Figure 1b shows a single frame of both sea lions engaged in coordinated swimming; and Figure 1C shows one sea lion engaged in activity, but neither sea lion is socially engaged. Faint broken lines signify borders for four of the five zones where the sea lion motor activity triggers the IP camera to record.

Table 1. California sea lions (*Zalophus californianus*) at The Marine Mammal Center (TMMC); MBO = Monterey Bay Operations, and SLO = San Luis Obispo Operations

ID number	Sex	Weight	Stranding date (d/mo/y)	Stranding location	Diagnosis at admittance	Dates observed
10357	M	21-32 kg	6/7/2012	Montana De Oro State Park (SLO)	Malnutrition, abscess	August 3
10361	F	20.5 kg	9/7/2012	Lampton Park Cambria (SLO)	Malnutrition, trauma	August 3
10398	M	22.5-29 kg	16/8/2012	Morro Bay Jetty (SLO)	Malnutrition, sloughed abscess, right carpal sepsis	September 11-12
10400	M	19-22.5 kg	18/8/2012	Sandspit (SLO)	Malnutrition, fractured skull	September 11-12
10412	M	34.5-46 kg	2/9/2012	Oceano Dunes Vehicular Recreation Area (SLO)	Gunshot causing trauma to eye and face, blindness in one eye	October 5-9, 24-31; November 1-8, 11-12
10413	M	Unknown	2/9/2012	Unknown	Leptospirosis	September 19-20
10420	M	36 kg	9/9/2012	Greyhound Dock	Malnutrition, leptospirosis	September 19-20, 27-29; October 2, 4
10421	M	84 kg	15/9/2012	Cowell (MBO)	Blind, presumed domoic acid exposure	September 27-29; October 2, 4-9
10426	M	26-34 kg	20/9/2012	Seaside Beach (MBO)	Abscess	October 6, 8-10, 12-13, 19, 23
10433	M	48.5 kg	26/9/2012	NSC Harbor-J Dock (MBO)	Leukocytosis, inflammation	October 19, 23
10434	F	29 kg	27/9/2012	Seacliff State Beach	Malnutrition, azotemia	October 6, 8-10, 12-13
10444	F	20.5-21.5 kg	7/10/2012	Beach in front of 7201 Highway 1 (MBO)	Malnutrition, verminous pneumonia	October 24-31; November 1-8
10457	M	37.5 kg	3/11/2012	Doran Beach Sonoma (Saus)	Malnutrition, renal disease, parafilaroides, tapeworms, flukes, pox on chin	November 11-12
10464	F	25 kg	7/11/2012	Port San Luis Pier (Hartford Pier) (SLO)	Malnutrition, pneumonia	November 26
10472	M	27 kg	22/11/2012	Carmel Beach (City State Beach), (MBO)	Malnutrition, pneumonia, harassment from humans	November 26

Also excluded were recordings of sea lion behaviors triggered by human activity such as arousal in anticipation of feeding. Recordings were compiled into video files identified by date and time of day (AM or PM). After trimming and compiling, a total of 58 video compilations remained, spanning 41 d, including 17 full days (days for which we had both AM and PM videos). One of these video files did not contain identifiable social behaviors. In total,

11 male and four female sea lions were observed. These 15 sea lions consisted of four mixed-sex dyads over 23 d and six male dyads over 18 d.

We developed two ethograms to evaluate behavior: (1) a Social Behavior Ethogram (Table 2) and (2) a control Behavioral Activity Ethogram for assessment of overall activity (Table 3). Social behavior requires the participation of at least two individuals, so we measured behaviors in the

Table 2. Social Behavior Ethogram

Behavioral Descriptions

Nose/Mouth: When sea lion (CSL) 1's nose or mouth either touches or is within one head length of the head—including muzzle—or neck of CSL 2 (or CSL 2 to CSL 1). The mouth may be either open or closed and can be initiated from any direction. Animals may be sitting, laying down, or swimming during this interaction.

Approach: When CSL 1 moves directly toward CSL 2 (or CSL 2 to CSL 1) to either interact with or be in closer proximity to that animal. The animal being approached may be sitting, laying/sleeping, swimming, or retreating from the second animal. This should also be scored when an animal in the water pops its head up over the pool rim in the direction of an animal on land. This behavior can originate either on land or in the water (see "Retreat" for more information). Do not score this if approaching animal has its attention toward the door or outside of the pen.

Retreat: When CSL 1 moves directly away from CSL 2 (or CSL 2 to CSL 1) by either running, walking, or jumping into the pool. This may be instigated by the social behaviors such as approach and nosing/mouthing. In instances when we need to distinguish between approach toward one animal and retreat from another, we will use the following protocol. If the first animal moves away from the second at a distance greater than two body lengths, this will be considered "retreat." If the first animal is moving toward the second and is within two body lengths, this will be considered "approach." This behavior may also include nose/mouth. This should not be scored if the retreating animal has its attention toward the door or outside of the pen.

Reciprocal Swimming: When CSL 1 is swimming in a coordinated fashion with CSL 2 (or CSL 2 with CSL 1). This involves lateral positioning of each animal within ½ body length, either head-to-tail or head-to-head, and can be either at the surface of the water or completely submerged. Movements may resemble twisting, tumbling, and mimicking each other's motions. This action may also include nosing and mouthing.

No Reaction: When CSL 1 or 2 makes no major bodily movement in response to an action initiated by the other animal. Animals may be lying down or upright but must not move more than one step in any direction, otherwise this should be scored as the appropriate behavior (e.g., following, retreat, etc.). When in the water, animals may be moving as long as there is no change in the speed or quality of the movement (e.g., acceleration or direction).

Coordinated Swimming: When both CSLs are in the water but are not engaging in the other defined social behaviors. The CSLs may be swimming in circles, past each other, or mirroring each other's movements.

Descriptions of Social Interactions

Approaching with Retreat: When CSL 1 moves directly toward CSL 2 (or CSL 2 to CSL 1) to either interact with or be in closer proximity to that animal and the second animal responds by retreating. This can occur either in the water or on land.

Approaching with No Reaction: When CSL 1 moves directly toward CSL 2 (or CSL 2 to CSL 1) to either interact with or be in closer proximity to that animal with no social response from the second animal. This can occur either in the water or on land.

Approaching with Nose/Mouth: When CSL 1 moves directly toward CSL 2 (or CSL 2 to CSL 1) to either interact with or be in closer proximity to that animal that responds by a nose/mouth interaction toward the first animal. This can occur either in the water or on land.

Approaching with Approaching: When CSL 1 moves directly toward CSL 2 (or CSL 2 to CSL 1) to either interact with or be in closer proximity to that animal, and it responds by moving toward the initiating animal. This can occur either in the water or on land.

Table 2 (cont.).

Approach with Reciprocal Swimming: When CSL 1 moves directly toward CSL 2 (or CSL 2 to CSL 1) to either interact with or be in closer proximity to that animal and that animal initiates reciprocal swimming in response. This can occur either when both animals are in the water or when one animal in the water approaches an animal on land that enters the water to initiate reciprocal swimming.

Retreat with No Reaction: When CSL 1 moves directly away from CSL 2 (or CSL 2 away from CSL 1) with no social response from the second. No reaction includes no head or body movement in response to the action of the first animal. This can occur either in the water or on land.

Retreat with Approaching: When CSL 1 moves directly away from CSL 2 (or CSL 2 away from CSL 1) and the second animal responds by following. This can occur either in the water or on land.

Nose/Mouth with Retreat: When CSL 1 noses/mouths toward CSL 2 (or CSL 2 to CSL 1) and the second animal retreats in response. This can occur either in the water or on land.

Nose/Mouth with No Reaction: When CSL 1 noses/mouths toward CSL 2 (or CSL 2 to CSL 1) with no response from the second. No reaction includes no head or body movement in response to the action of the first animal. This can occur either in the water or on land.

Nose/Mouth with Nose/Mouth: When CSL 1 noses/mouths toward CSL 2 (or CSL 2 to CSL 1) and the other noses/mouths in response. Noses and mouths may touch or be within two head lengths during this interaction. This can occur either in the water or on land.

Nose/Mouth with Reciprocal Swimming: When CSL 1 noses/mouths toward CSL 2 (or CSL 2 to CSL 1) and the second initiates reciprocal swimming. This can occur either when both animals are in the water or when one animal in the water noses/mouths an animal on land that enters the water to initiate reciprocal swimming.

Into Pool with Approach: When CSL 1 jumps into pool and CSL 2 reacts by either getting into the pool or moving in a position closer to the animal in pool (or CSL 2 to CSL 1). The second animal can either be in the water or on land.

Table 3. Behavioral Activity Ethogram

Total Land Activity for CSL 1

Total Land Activity for CSL 2

Total Land Activity includes all movements during which the CSL takes at least four steps toward a location. Coding begins on the second step. Coding ends when the CSL comes to a complete stop for at least 2 s.

Total Water Activity for CSL 1

Total Water Activity for CSL 2

Total Water Activity includes all movements during which the CSL moves at least half a body length. Coding ends when the CSL exits the water or stops moving for at least 2 s.

Nonsocial Activity for CSL 1

Nonsocial Activity for CSL 2

Nonsocial Activity is coded over Total Activity.

In water, Nonsocial Activity is coded when at least 1 CSL is swimming, but they are not engaging in coordinated swimming OR any specific social behaviors. Examples: (1) When one CSL is floating in the corner and the other CSL is swimming around the pool or (2) when one CSL is floating in the pool and the other CSL is swimming past but not engaging in approach or retreat.

On land, Nonsocial Activity is coded when activity occurs out of approach or retreat range.

Timestamp Code

A time stamp is used to note start times of periods of activity, people in pen, mealtimes, and video skips. It is also used to mark when the camera was on but no movement is occurring so that we know that the camera was working.

context of interactions of a pair. We can assess the behaviors of an individual by observing them interact with a variety of partners. For the Social Behavior Ethogram, we classified social behaviors that were expressed in 57 of the 58 video files and were scored as interactions of the sea lion pair such as approach–retreat. We identified key social behaviors: nose/mouth, approach, retreat, and reciprocal swimming (see "Behavioral Definitions" in Table 2). These behaviors were measured within a social encounter. Each measured behavior also captured the response of the other sea lion. For example, the code "approach–retreat" would begin with the presence of an approach behavior by sea lion A and would end at the completion of a retreat behavior by sea lion B. We also measured coordinated swimming, which captured simultaneous social behaviors of a pair such as swimming in a circle or mirrored movements.

A second ethogram was developed to control for the possibility that differences in social activity expressed by sea lions reflected overall behavioral activity rather than socially responsive behaviors. For this Behavioral Activity Ethogram (Table 3), we measured total activity on land and water and nonsocial activity. On land, total activity was recorded each time an individual took more than four steps to capture locomotion around the pen and to minimize capture of superficial movements such as scooting and rolling. In the water, movement was captured when an individual moved at least half a body length to minimize capture of superficial movements such as floating. In this second ethogram, social activity for each sea lion was calculated by subtracting the duration of all nonsocial behavioral activity from the duration of all activity. Percent social behavior was calculated by dividing total calculated social activity by total activity.

Observers scored frequency and duration of behaviors with *VCod*e software (Version 1.2.1, University of Illinois, Urbana, IL, USA). To score video-recordings, keyboard keys were pre-assigned for behaviors or set of behaviors present in the ethogram (Tables 2 & 3) and pressed at the start of the specified activity. The same corresponding key was pressed again when the behavior ceased. To track start times, we created a code called "Timestamp" that was coded at the start of a period of activity and after any lapses in the video. Time stamps were coded at discrete points in time and allowed us to manually add the local time visible on the camera recordings. Time stamps were also used to identify times when pens were being cleaned or sea lions fed to avoid misrepresenting these times when humans were present as times when animals were inactive. Data from *VCode* was saved as .csv files and exported for analysis in *SPSS*.

Video recordings were collected over 116 d from 3 August to 26 November. To control for seasonal variations in the position of the sun, we measured behaviors in the context of sun position. This approach also makes sense in terms of sea lion experience of the progression of the day rather than by mechanical time, which is a human invention. Our analyses were collected into time bins according to each day's sunrise, solar noon, and sunset as well as the midpoints between sunrise and solar noon and solar noon and sunset (see www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html), resulting in a total of six time periods: (1) pre-sunrise, (2) early AM, (3) late AM, (4) early PM, (5) late PM, and (6) post-sunset. We found little activity before sunrise, so this time period was removed from our analyses.

We compared social behaviors of males vs females in dyads (mixed-sex or all-male) and individuals in different housing arrangements (male subjects with female objects, male subjects with male objects, and female subjects with male objects). We lacked sufficient video recordings for female dyads. We also analyzed four pairs of sea lions made up of six individuals (#10412, #10420, #10421, #10426, #10434, and #10444) for at least 3 d each to look at individual differences. Additionally, we compared social activity of one pair (#10412 and #10444) over 15 d of observation to look for changes in sociality over the recovery period.

To evaluate the proportion of activity that these four pairs of sea lions expressed that was social vs other active behaviors, we divided coordinated swimming by total activity. We also divided specific social behaviors (approach, retreat, nose/mouth, and reciprocal swimming) by the sum of all social behavior to identify preferred behaviors.

Statistical analyses included independent sample *t* tests and one-way ANOVAs. These tests were used to compare mean frequencies and durations of various activities between either individual sea lions or dyads and times of day. A *post-hoc* Tukey test was used to specify significant differences. Means were calculated for full days as well as for each time period.

Results

Using the Social Behavior Ethogram (Table 2), we first asked whether social behaviors of mixed-sex and male interactions varied with time of day. The average total number of social interactions per day of mixed-sex (Mean [M] = 52.50, Standard Deviation [SD] = 32.34) and male pairs (M = 97.40, SD = 55.78) did not significantly differ (independent *t* test, $t(13) = -2.01$, $p = 0.065$). Similarly, the average duration each day engaged in social interactions within mixed-sex (M = 205.29 s, SD = 113.09 s) and male (M =

339.06 s, SD = 185.27 s) pairs was not found to differ (independent *t* test, $t(13) = -1.48, p = 0.103$). However, we found that mixed-sex and male interactions differed in the time of day when they engaged in social activity. Mixed-sex interactions occurred more frequently in the early AM (M = 118.14 s, SD = 148.82 s) and less frequently as the day progressed (late AM: M = 59.94 s, SD = 47.20 s; early PM: M = 52.41 s, SD = 43.93 s; late PM: M = 13.80 s, SD = 14.91 s; and post-sunset: M = 20.84 s, SD = 15.28 s) (one-way ANOVA, $F(4, 53) = 2.694, p = 0.041$). By contrast, social interactions within male pairs did not signifi-cantly change with time of day (early AM: M = 81.63 s, SD = 74.00 s; late AM: M = 95.66 s, SD = 171.85 s; early PM: M = 80.97 s, SD = 69.52 s; late PM: M = 83.46 s, SD = 113.27 s; and post-sunset: M = 39.70 s, SD = 48.08 s) (Figure 2).

We then asked how specific social behaviors (approach, retreat, nose/mouth, reciprocal swim-ming, and coordinated swimming) coded in our Social Behavior Ethogram varied across sex and time of day. On average, male pairs participated in a greater frequency of approach interactions per day (M = 54.40, SD = 19.93) than mixed-sex pairs (M = 24.50, SD = 16.74) (independent *t* test, $t(13) = -3.07, p = 0.009$). Similarly, male pairs spent a longer average duration of time in approach interactions per day (M = 159.34 s, SD = 45.87 s) than mixed-sex pairs. (M = 79.48 s, SD = 53.82 s) (independent *t* test, $t(13) = -2.83, p =$

0.014) (Figure 3). Sea lions did not adjust their patterns of approach throughout the day by fre-quency (one-way ANOVA, $F(4, 92) = 1.427, p = 0.231$) or duration (one-way ANOVA, $F(4, 92) = 1.384, p = 0.246$).

Mixed-sex and male pairs did not significantly differ in the average frequency of nose/mouth behaviors per day (mixed-sex: M = 15.90, S = 9.46; male: M = 33.40, S = 29.48; independent *t* test, $t(13) = -1.76, p = 0.102$) over the 15 full days in which nose/mouth interactions occurred, nor did they differ in the average duration of nose/mouth interactions per day (mixed-sex: M = 56.72 s, S = 36.33; male: M = 108.04 s, S = 101.65; indepen-dent *t* test, $t(13) = -1.47,- p = 0.167$). Sea lions did not adjust their patterns of nose/mouth interac-tions throughout the day by frequency (one-way ANOVA, $F(4, 71) = 0.827, p = 0.512$) or duration (one-way ANOVA, $F(4,71) = 0.623, p = 0.648$).

Mixed-sex and male pairs did not significantly differ in the average frequency of retreat behav-iors per day (mixed-sex: M = 18.60, S = 12.10; male: M = 25.00, S = 11.51; independent *t* test, $t(13) = -0.98, p = 0.345$) over the 15 full days in which retreat interactions occurred, nor did they differ in the average duration of retreat interac-tions per day (mixed-sex: M = 89.38 s, S = 52.94; male: M = 116.04 s, S = 53.20; independent *t* test, $t(13) = -0.92, p = 0.375$). Sea lions did not adjust their patterns of retreat interactions throughout the day by frequency (one-way ANOVA, $F(4, 86) =$

(a) (b)
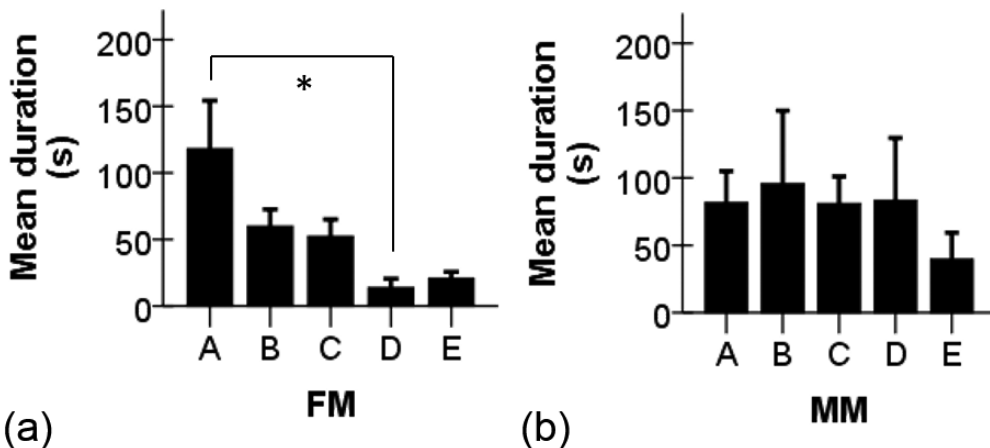
Figure 2. Durations of dyadic social activity vary with time of day in mixed-sex pens. Duration is reported in seconds (s). Daylight hours were divided into five segments: (A) early AM, (B) late AM, (C) early PM, (D) late PM, and (E) post-sunset. FM refers to mixed-sex dyads, and MM refers to all-male dyads. Error bars represent one standard error (SE). (a) Sea lions in mixed-sex dyads spent more time in social interactions during the morning and decreased in social activity as the day progressed. A one-way ANOVA with a Tukey post-hoc shows that there is a significant difference in duration between early AM (A) and late PM (D), $p = 0.041$. (b) Sea lions within male dyads spent similar amounts of time in social interactions irrespective of time of day.

1.328, $p = 0.266$) or duration (one-way ANOVA, $F(4, 86) = 1.339, p = 0.262$).

Though both reciprocal swimming and coordinated swimming are highly social behaviors that require direct participation of each sea lion, we found very different results. Mixed-sex and male pairs did not significantly differ in the average frequency of reciprocal swimming per day (mixed-sex: $M = 4.33$, $S = 2.18$; male: $M = 4.75$, $S = 3.40$; independent t test, $t(11) = -0.27, p = 0.792$) over the 13 full days in which reciprocal swimming occurred, nor did they differ in the average duration of reciprocal swimming per day (mixed-sex: $M = 24.41$ s, $S = 17.30$; male: $M = 28.52$ s, $S = 21.92$; independent t test, $t(11) = -0.37, p = 0.721$). Sea lions did not adjust their patterns of reciprocal swimming throughout the day by frequency (one-way ANOVA, $F(4, 40) = 0.741, p = 0.569$) or duration (one-way ANOVA, $F(4,40) = 1.04, p = 0.397$). By contrast, male pairs spend much more time per day in coordinated swimming than mixed-sex dyads (male: $M = 2,681.29$ s, $SD = 2,200.27$ s; mixed-sex: $M = 178.08$ s, $SD = 294.07$ s; independent t test, $t(15) = -4.04, p = 0.001$) (Figure 4). Coordinated swimming did not fluctuate significantly throughout the day (one-way ANOVA, $F(4, 228) = 1.640, p = 0.165$).

To determine whether sea lion social activity reflected intrinsic variations in social motivation or was instead a manifestation of more general behavioral activity, we developed a Behavioral Activity Ethogram (Table 3). The average total behavioral activity per day for males ($M = 3,091.05$ s, $SD = 3,852.95$ s) more than doubled

that of females ($M = 1,270.02$ s, $SD = 1,339.86$ s), but these averages were not significantly different (independent t test, $t(27) = -1.57, p = 0.129$). However, when males were housed with other males, averages of total behavioral activity per day ($M = 7,734.14$ s, $SD = 3,863.50$ s) were considerably more active than males housed with females ($M = 1,156.43$ s, $SD = 1,510.96$ s), or females housed with males ($M = 1,270.02$ s, $SD = 1,339.86$ s) (one-way ANOVA, $F(2, 26) = 21.885$, $p < 0.001$; Tukey *post-hoc*, $p < 0.001$) (Figure 5).

When both sexes were considered, overall sea lion activity was greatest in the early AM time period ($M = 710.81$ s, $SD = 980.42$ s) and least in the post-sunset time period ($M = 119.36$ s, $SD = 310.74$ s), with activity levels during late AM ($M = 413.28$ s, $SD = 670.01$ s), early PM ($M = 410.79$ s, $SD = 505.80$ s), and late PM ($M = 543.20$ s, $SD = 1,191.48$ s) falling in between (one-way ANOVA, $F(4, 228) = 4.08, p = 0.003$) (Figure 5). We found no interaction effect between sex dyad and time of day (2×2 factorial ANOVA, $F(8, 218) = 0.778, p = 0.622$).

Sea lions within all dyad contexts spent a greater proportion of their activity in social interactions during post-sunset hours ($M = 40.39\%$, $SD = 38.27\%$). The lowest proportion of social activity/total activity occurred in late PM ($M = 16.79\%$, $SD = 25.78\%$). Intermediate levels of social activity/total activity occurred during midday: early AM ($M = 31.38\%$, $SD = 25.51\%$), late AM ($M = 27.63\%$, $SD = 30.14\%$), and early PM ($M = 30.96\%$, $SD = 27.91\%$) (one-way ANOVA, $F(4, 228) = 2.703, p = 0.031$) (Figure 6). The proportion of total behavior that is social does not significantly differ between
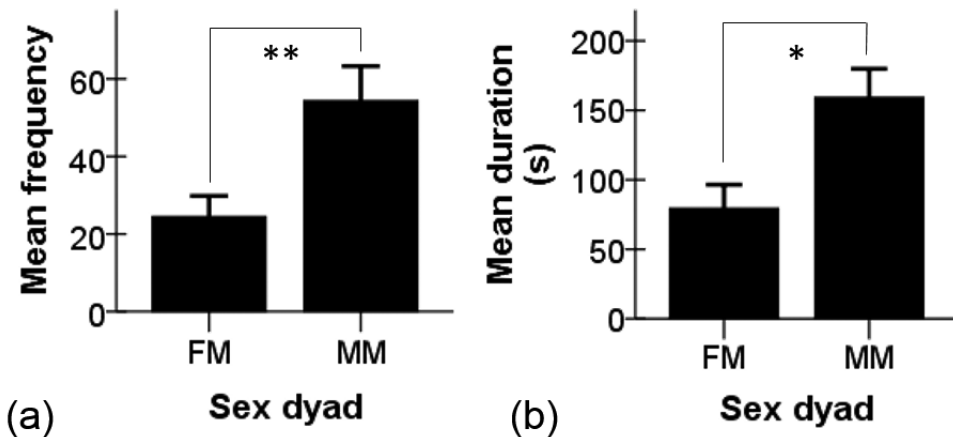
Figure 3. Mixed-sex and male dyads differ in the amount of social approach per day. FM refers to mixed-sex dyads, and MM refers to all-male dyads. In Figure 3b, duration is reported in seconds (s). Error bars represent 1 SE. (a) A t test showed that all-male dyads approached conspecifics significantly more times per day than mixed-sex dyads, $p = 0.009$. (b) Similarly, a t test shows that all-male dyads spent more time per day in interactions involving approach than mixed-sex dyads, $p = 0.014$.
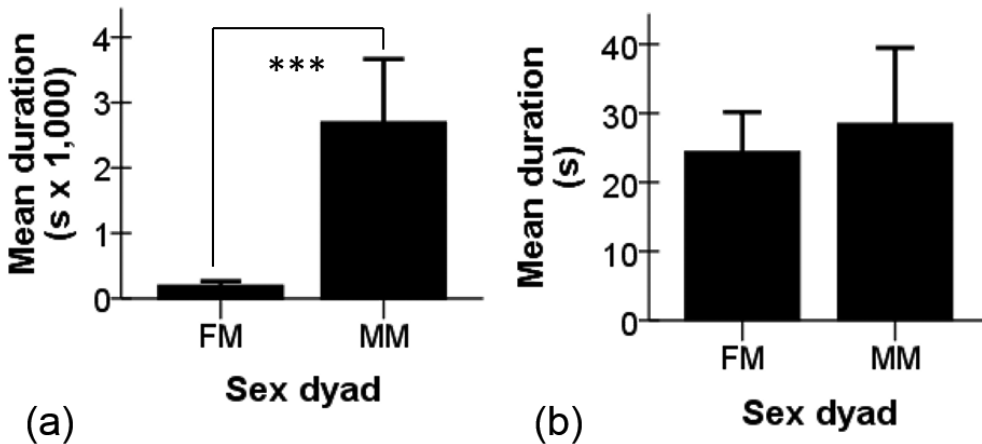
Figure 4. Male dyads participate in more coordinated swimming per day than mixed-sex dyads but not in reciprocal swimming. FM refers to mixed-sex dyads, and MM refers to male dyads. Error bars represent 1 SE. (a) Duration is reported in thousands of seconds (s × 1,000). A *t* test shows that males housed with males participated in significantly more coordinated swimming than females housed with males, $p = 0.001$. (b) Duration is reported in seconds (s). In contrast, there was not a significant difference in the amount of reciprocal swimming between mixed-sex and male dyads.

males housed with males (M = 45.82%, SD = 24.60%), males housed with females (M = 28.53%, SD = 17.27%), or females housed with males (M = 28.44%, SD = 18.42%) (one-way ANOVA, $F_{(2, 26)} = 1.713, p = 0.200$).

Given overall patterns, we were interested in looking at how patterns of behavior vary among specific individuals. We identified four dyads of sea lions for whom we have more than 3 d of footage and ended up with four dyads made up of six individuals. Because we had seen such strong variation in the amount of coordinated swimming per day, we looked at that first. We found a significant difference between specific dyads in the proportion of total activity that is coordinated swimming (one-way ANOVA, $F_{(3, 21)} = 3.447, p = 0.035$) on days in which coordinated swimming occurred. A *post-hoc* Tukey test showed that #10412 and #10421 spent a larger proportion of their total activity per day in coordinated swimming (M = 38.95%, SD = 10.95%) than #10412 and #10444 (M = 12.27%, SD = 12.79%) (*post-hoc* Tukey, $p = 0.037$), with #10426 and #10434 (M = 18.94%, SD = 8.49%) and #10420 and #10421 (M = 29.29%, SD = 26.60%) falling in between (Figure 7).

A one-way ANOVA showed a significant difference between pairs for the proportion of dyadic social activity that included approach behavior for both duration (one-way ANOVA, $F_{(3, 27)} = 3.88, p = 0.020$) and occurrence (one-way ANOVA, $F_{(3, 27)} = 4.53, p = 0.011$) rate. A *post-hoc* Tukey test shows that #10420 and #10421 spent more of their social activity in approach interactions (M = 57.63%, S = 6.63)
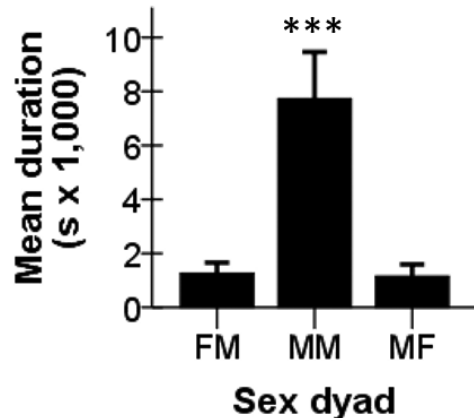
**Figure 5.** Males housed with males are more active than males housed with females. Duration is reported in thousands of seconds (s × 1,000). FM refers to females housed with males, MM refers to males housed with males, and MF refers to males housed with females. Total activity was collected for each individual sea lion. Error bars represent 1 SE. A one-way ANOVA shows that males housed in male dyads expressed more behavioral activity per day than males housed in mixed-sex dyads or females housed in mixed-sex dyads, $p < 0.001$.

than #10426 and #10434 (M = 33.45%, S = 10.88) (Tukey *post-hoc*, $p = 0.020$) (#10412 & #10421: M = 48.85%, S = 8.26; #10412 & #10444: M = 41.29%, S = 14.04). Sea lions #10420 and #10421 also participated in more approach interactions per dyadic interactions when looking at
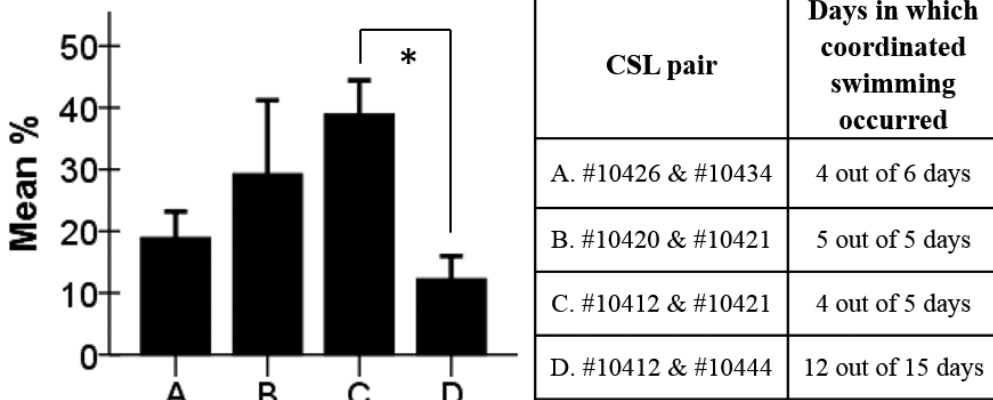
the number of interactions (M = 64.76%, S = 9.44) than #10426 and #10434 (M = 41.01%, S = 7.74) (Tukey *post-hoc*, p = 0.010) (#10412 & #10421: M = 56.50%, S = 7.90; #10412 & #10444: M = 49.63%, S = 12.62) (Figure 8). All pairs participated in approach interactions every day they were filmed.

Discussion

Sea lions arrive at TMMC afflicted with infections, injuries, poisoning, and malnutrition. With such a range of conditions, their degrees of illness and recovery can be difficult to assess. Recent studies show that sea lion habituation and repetitive behaviors can be responsive to domoic acid
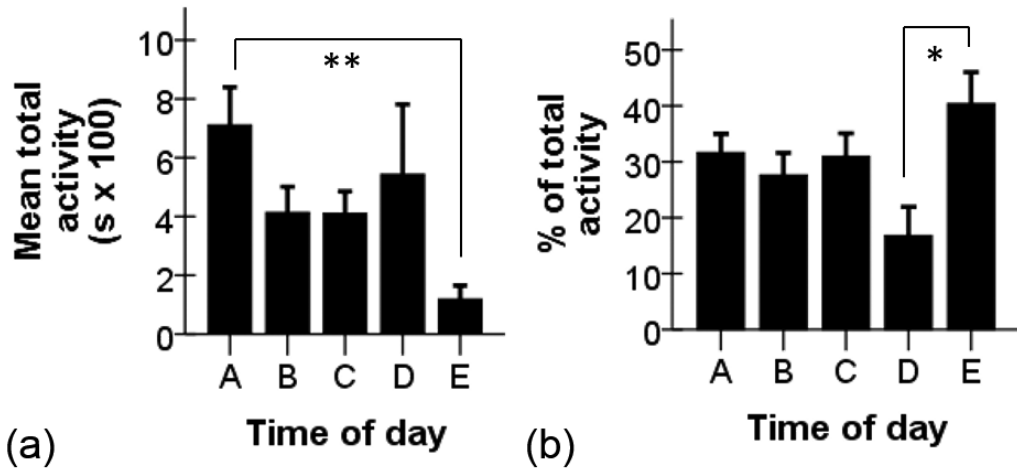
Figure 6. Sea lions are most active early in the day, but they are proportionately more social late in the day. A = early AM, B = late AM, C = early PM, D = late PM, and E = post-sunset. Error bars represent 1 SE. (a) Duration is reported in hundreds of seconds (s × 100). A one-way ANOVA with a post-hoc Tukey test shows that sea lions were the most active in the early AM (A) and the least active during post-sunset (E), p = 0.003. (b) Percentages were calculated as total duration of social behavior divided by total duration of behavioral activity for each time period and each day. A one-way ANOVA with a post-hoc Tukey test shows that sea lions were proportionately more social during post-sunset (E) compared to late PM (D), p = 0.031.

CSL pair	Days in which coordinated swimming occurred
A. #10426 & #10434	4 out of 6 days
B. #10420 & #10421	5 out of 5 days
C. #10412 & #10421	4 out of 5 days
D. #10412 & #10444	12 out of 15 days

Figure 7. Specific dyads preferred coordinated swimming. Rates were calculated by dividing total behavioral activity by duration of coordinated swimming for each day a pair participated in coordinated swimming. Error bars represent 1 SE. A one-way ANOVA shows that the rates of coordinated swimming significantly differed among individual pairs. Sea lions #10412 and #10421 participated in proportionately more coordinated swimming per day than sea lions #10412 and #10444, p = 0.035.
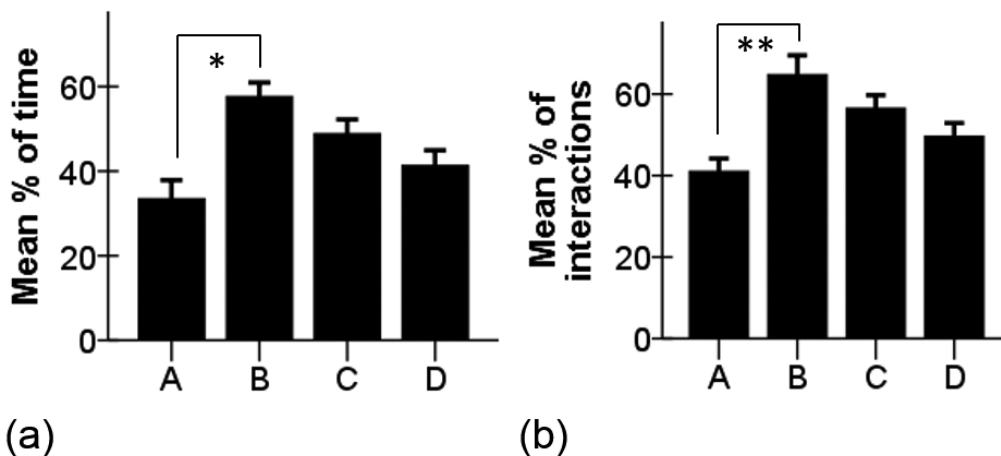
Figure 8. Specific dyads preferred approach. A = #10426 & #10434, B = #10420 & #10421, C = #10412 & #10421, and D = #10412 & #10444. Each of these sea lion pairs displayed approach interactions every day they were viewed. Percentages were calculated as duration of approach interactions over duration of social interactions, and number of approach interactions over number of interactions. Error bars represent 1 SE. (a) The percentage of social activity including approach varied among individual pairs. A one-way ANOVA shows that #10420 and #10421 spent proportionately more time in approach interactions compared to other dyadic social interactions than #10426 and #10434, $p = 0.020$. (b) A one-way ANOVA shows that #10420 and #10421 also displayed proportionately more approach interactions compared to other dyadic social interactions than #10426 and #10434, $p = 0.010$.

exposure (Cook et al., 2011; Wittmaack et al., 2015). We believe that social behavior may also be a tractable indicator of health and illness. Our long-term goal is to use an objective evaluation of social behavior as a metric of recovery. Since veterinary centers are sometimes inundated with incoming patients, and staff have little time each day to observe individuals, our objectives in this initial phase are (1) to develop an ethogram for social behavior as well as an ethogram to control for overall behavioral activity and (2) to gain a general sense for how social behaviors vary according to sex and time of day in a recovering population of sea lions. With these data, we could identify optimal times of day (ideally less than 1 h of recording) to videotape sea lions. Since immature California sea lions are frequent patients of TMMC, we chose to develop our ethograms and make our initial assessments with this age group.

We found discernible patterns of sociality in immature sea lions recovering in pens at TMMC. Sea lions in pens that included females were more socially active in the morning and became gradually less active as the day progressed. The frequency of social interactions among males did not change throughout the day. Overall, male subjects were more physically active and approached conspecifics more often than did females. Coordinated swimming was significantly more common among male dyads than among mixed-sex dyads. These results bare resemblance to findings of rough-and-tumble play among juvenile rodents, particularly male rats (Siviy & Panksepp, 1985; Pellis & Pellis, 1997) and squirrels (Steiner, 1971; Lahvis et al., 2015). However, reciprocal swimming, more similar to rough-and-tumble play than coordinated swimming with its robust and rapidly interactive movements, showed no sex-specific differences.

Variations of individual behavior are influenced by many factors, ranging from sex and age to temperament and relative health (e.g., the nature of the illness, the specific drug treatment, and the time spent recovering). Further, it can be challenging to develop an ethogram that encompasses the variety of symptoms and behaviors present in a recovering population. In our sample, some of the dyads had preferred behaviors; they would engage in a particular interaction much more frequently than other pairs. For example, sea lion #10421 engaged in more coordinated swimming when paired with #10412 but preferred approach interactions when paired with #10420.

It is important to note that the Social Behavior Ethogram is used to record reciprocated interactions of pairs, both the social behavior of a single individual and a social response from the other participant. Thus, we were unable to generate separate scores for each individual. For instance, sea lions #10420 and #10421 show a preference for approach interactions as a pair, but we do not

know which individual initiated the interaction. It is possible that #10421 may have simply reacted to the repeated approach behaviors of sea lion #10420 or vice versa. We also are unable to decipher whether an increased frequency of approach behavior expressed by a particular sea lion subject toward another individual represents a propensity for approach by the subject or greater solicitous communication expressed by the individual approached. To dissociate the social behavior of an individual sea lion from the effects unique to the pair, future studies would benefit from linked ethograms that assess both dyadic social interactions and individual social behaviors.

We expect sea lion social behavior to become more robust with recovery, but we were unable to confirm such changes in the current study because each of our subjects was housed with a variety of social partners while they resided at TMMC. Our longest period of observation for a single sea lion pair (#10412 & #10444) consisted of an 80-d recovery for #10412 and just 15 d of a 33-d recovery for #10444. We did not find the social activity for this dyad to differ between the first and second weeks of observation. Rather, we found tremendous daily variation over this observed period. Critically, #10444 restranded shortly after release, so the lack of observable improvement in social behavior may be consistent with this individual's lack of full recovery. We observed other sea lions for even shorter fractions of their total recoveries. For example, #10421, who was ultimately euthanized for blindness due to presumed domoic acid exposure, was observed for 8 d (and housed with two different individuals) during a 26-d stay at TMMC. Of interest is whether #10421's preference for coordinated swimming when housed with #10412 vs the preference for approach when housed with #10420 can be attributed to the health state of #10421 in the days prior to euthanasia for this individual or to the respective preferences of co-housed individuals. Use of social interaction assessments for evaluation of sea lion recovery would require housing of specific pairs of sea lions together for a set period of time to observe them at more separated time points across their recovery period. To further explore the relationship between social behaviors and recovery status, ongoing evaluations should also integrate our metrics for social behavior with other diagnostic measures.

With the exception of one individual (#10421), sea lions observed in this study were released into the wild after they were deemed to be recovered from the malnourishment, illness, or injury presented upon admission. Sea lion #10421 was admitted to TMMC with suspected ("presumed domoic acid exposure") and neurosensory damage that caused intermittent blindness, eventually resulting in euthanasia. Given the sensitivity of social interactions to disability, we found it surprising that #10421 participated in dyadic interactions similar to levels expressed by other participants. Explanations include the possibility that intermittent vision loss was only infrequent or perhaps that social approach behavior does not require good vision. While #10421 had not yet reached adulthood, this individual had a larger body size compared with other individuals housed within the same pen. It is unclear how body size could potentially affect the dynamics of a pair among immature sea lions in pens used for recovery.

Sea lion behaviors in recovery pens are not analogous to behaviors expressed in natural habitats. Walls and limited space, scheduled feeding times, and human contact alter the context for expression of social behavior. It is axiomatic that lack of social refuge, unnatural foraging opportunities, access to exploration, and unnatural variations in habitat will influence the nature of social interactions (Lahvis, 2016, 2017a). The behavioral patterns we observed have practical implications for understanding sea lion recovery, but they may have limited value for predicting behaviors in a natural environment. For instance, many of the individuals faced the doors prior to mealtime, which may have temporarily altered their social behaviors.

One limitation includes our use of the video retrieval technology, which precluded continuous sampling across all days of our study period. Cameras occasionally malfunctioned by triggering to begin recording in the middle of an action rather than at its start. Our data still represents a sample of days and times during the sea lions' stays at TMMC but was neither a true random sample nor a scheduled sample. In future studies, sampling-specified durations of time at set points throughout the day will improve temporal consistency of recordings and avoid times influenced by feedings and other human contact.

Our results indicate that optimal times for immature sea lion observations are in the morning or early afternoon for males and in the morning for females. Though both sexes expressed lower levels of activity post-sunset compared to earlier time periods, a larger proportion of their behavior activity at evening twilight were social. Future data collections at these time periods would allow for more efficient evaluation of sea lion sociality. When combined with other measurements of health (e.g., blood tests, antibody tests, weight, etc.) during a recovery period, we could assess the subtle effects of a health condition on sociality and use these measures of social behavior to assess recovery.

Taken as a whole, we find that the social behaviors of California sea lions, under the constrained

conditions imposed by recovery, offer a tremendous opportunity for exploring the relationship between individual temperament and the social dynamics of the group. Study of these recovering sea lions also offers us opportunities to understand the neurobiology of social interaction under developmental conditions that afford research subjects opportunities for social refuge and a range of cognitive and affective experiences, not unlike human experiences. While we will never know the developmental histories of individuals that come to TMMC, we can be certain they experienced decision-making opportunities and consequences for their decisions—conditions not afforded to experimental animals living under highly constrained caged conditions with no opportunity for cognitive or affective development (Lahvis, 2016, 2017a). Life-long captivity of laboratory rodents and primates inside cages and corrals can promote abnormalities that are widespread across biological systems (Lahvis, 2017b). While our observations mark only a small step toward more rigorous study of recovering sea lion social behavior, they serve as a foundation for future studies of complex social interaction in this remarkably intelligent species (see Kastak et al., 2001).

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