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Case Studies of Bear Cub Development Under Unique Rearing Conditions

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Abstract – Zoo-based polar bear (*Ursus maritimus*) literature is heavily biased towards reproduction and neonate development, or the behavioral management of adult individuals, often excluding the critical juvenile developmental period between den emergence and adulthood. The birth of two female cubs (Astra and Laerke) at the Detroit Zoo in 2020, and their subsequent divergent rearing conditions, offered a unique opportunity to document their development. Astra remained with her mother, Suka, to be parent-reared while Laerke was removed from Suka's care and hand-reared due to medical necessity. Laerke was temporarily housed with a male grizzly bear (*Ursus arctos horribilis*) cub (Jeb), a wild-born orphan of approximately the same age, brought to the Detroit Zoo so that he and Laerke could be reared socially together. We conducted 119 hr of focal behavioral follows totaling 470 observations across a 14-month period. This allowed us to investigate Astra's developmental trajectory and Laerke and Jeb's behavioral responses to co-housing. Astra demonstrated increased maternal independence throughout the study period. During the period when Astra and Laerke both had access to a social partner, Laerke demonstrated higher rates of social and undesirable behaviors than Astra. However, they demonstrated no significant variation in their time spent in behaviors such as swimming, independent play, investigation, and patterns of social proximity. This monitoring also allowed us to identify when Laerke and Jeb's developmental trajectories began to branch, and cross-species housing was no longer indicated. Documentation of these cubs and their unique housing conditions may be beneficial to institutions faced with hand-rearing cubs in the future.

Keywords – Social housing, Polar bear, Grizzly bear, Cub development, Behavior

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As of 2022, the polar bear (*Ursus maritimus*) population housed within institutions accredited by the Association of Zoos and Aquariums (AZA) was limited to 52 individuals with an actual U.S. breeding population of 26 individuals overseen by the Bear Taxon Advisory Group (TAG) (Jungheim, 2022). The AZA also oversees a population of approximately 118 individuals of brown bear species (*Ursus arctos*) monitored by the Bear TAG, though neither species currently have their own Species Survival Plan (SSP) (Vineyard, 2023). The brown bear population is a strictly non-breeding population, as population sustainability is achieved by the U.S. Fish and Wildlife Service placing orphaned cubs in AZA facilities for long-term care (Vineyard, 2023). The brown bear population has remained stable and hardy, making them a lower priority for reproductive and developmental research compared to other less stable bear species. In contrast, the AZA polar bear population initially demonstrated high and consistent growth rates, with a mid-1970's peak of 200 individuals in the managed population, but the population slowly declined at an average rate of 3.5% per year between 2017 and 2022 (Jungheim, 2022). Polar bear cub survival both *in* and *ex situ* increases with age (AZA Bear TAG, 2009; Che-Castaldo & Meyerson, 2019; Demaster &

Stirling, 1983; Ramsay & Stirling, 2009). Thus, lowering first-year mortality and increasing population growth are priorities for polar bear management, both in captive and wild settings (Che-Castaldo & Meyerson, 2019; Vineyard, 2023).

In the wild, females typically enter the den between October and December (Smith, 2021) and initially emerge with surviving cubs between March and April (Jonkel et al., 1972). At the time of den emergence, cubs are generally five to six months of age. The maternal unit may remain at the den site for a further one to four weeks following the initial emergence (Jonkel et al., 1972). After abandoning the den, but prior to independence at one to two years of age (depending on the study site), the maternal unit will travel the sea ice, during which time the cubs continue to develop and learn critical hunting skills (Stirling, 1990; Stirling & Latour, 1978). However, it is nearly impossible to track units over the sea ice. As such, it is currently unclear what behavioral and developmental processes cubs experience during this maturation stage. Thus, the extensive period following den emergence and abandonment, but preceding maternal independence, is understudied in both wild and captive polar bear populations but is thought to be one of the most difficult periods of a polar bear's life (Stirling, 2011).

Captive environments, such as accredited zoos, may provide an opportunity to investigate behavioral development as cubs grow to independence, but these data have only been sparsely reported for zoo-housed individuals. The vast majority of zoo-based polar bear research focuses on either the neonate period (Deun, 1961; Gartland et al., 2023; Hess, 1971; Kenny & Bickel, 2005; Michalowski, 1971; van Gessel, 2015; Wortman & Larue, 1974) or behavioral management of adult individuals (Cless & Lukas, 2017; Curry et al., 2015; Kelly et al., 2015; Renner & Kelly, 2006; Ross, 2006; Shepherdson et al., 2013; Skovlund et al., 2023a; Skovlund et al., 2023b). We see a similar focus on the care and welfare of adult individuals when surveying zoo-based brown bear literature (Andrews & Ha, 2014; Berghammer, 2008; Fernandez et al., 2020; Fuller et al., 2021; McGowan et al., 2010). In a rare captive study of the den emergence period in polar bears, Greenwald and Dabek (2003) focused on a cub aged four to twelve months old and emphasized patterns of swimming and behaviors potentially related to the evolution of the mother-cub relationship. They concluded that social separation of mother and cub should be delayed as much as possible to ensure healthy social and behavioral development (Greenwald & Dabek, 2003).

Mother-rearing of yearling ursids is encouraged whenever possible (AZA Bear TAG, 2009), but when this is not possible it is recommended that individuals be reared with conspecifics (King & Mellen, 1994; Meder, 1992; Reichard et al., 1990). Across mammalian taxa, social deprivation or inappropriate socialization in infants and immature individuals may have detrimental effects on behavioral development including development of undesirable behaviors or asociality, failure to learn proper sexual posturing, or complete lack of sociosexual behavior (Erwin & Deni, 1979; Harlow & Harlow, 1962; Latham & Mason, 2008; Mitchell et al., 1979; Powell, 2010; Ryan et al., 2002). Captive-born cubs that are unable to be mother-reared may transfer between institutions to facilitate social housing, particularly if the receiving facility can house the cub with similar age-mates (AZA Bear TAG, 2009). Due to strict regulations around bringing wild-born orphaned polar bear cubs into captivity ("The Marine Mammal Protection Act," 1972) and low captive birth rates, there can be limited opportunities for socialization for hand-reared singleton polar bear cubs. In contrast, wild-born orphaned or rescued grizzly bear cubs are increasingly rescued and rehabilitated for release or placed in long-term human care allowing for greater opportunities for proper socialization (Beecham et al., 2016; Jonkel et al., 1980; Kolter & van Dijk, 2000; Komnenou et al., 2018). Socially housing polar bear cubs with other bear species could potentially help meet their physical, cognitive, and emotional needs, but this practice requires further study.

Developmental data collected in zoological settings can provide critical insight into the environmental conditions necessary to support healthy socio-physical development, improving both population sustainability and individual animal welfare. This type of literature for brown bears is very sparse, likely due in part to the fact that these species are not bred in zoos. Additionally, literature related to orphaned or rescued cubs tends to focus on rehabilitation and release (Beecham et al., 2016; Kolter & van Dijk, 2000; Sheldon et al., 2022). However, the birth of two female polar bear cubs, one mother-reared (Astra) and one hand-reared (Laerke), at the Detroit Zoo in 2020 has offered an opportunity for long-term developmental study. Continuous monitoring of Astra during her first 12 weeks (approximately three months) provided valuable developmental data on nursing, activity, and maternal proximity (Gartland et al., 2023). The second installment of this study focused on the period immediately surrounding den emergence (ages 14-24 weeks; approximately 3-5 months) and allowed for comparisons of circadian rhythms and behavioral patterns between Astra and Laerke (Gartland et al., 2024). We were able to establish remarkably similar patterns in inactivity, locomotion, and independent play between the two cubs, as well as track Astra's growing independence from her mother and successful mitigation of stereotypic behaviors in Laerke. The third installment tracked endocrine measures, specifically fecal glucocorticoid metabolite concentrations, over time, across social conditions, and in relation to behavioral and environmental patterns (Bovee et al., 2025). Given their rearing conditions, this litter has provided further insight into the differing needs of cubs based on their social conditions.

The final installment of this study, as presented here, was focused on social and behavioral development of both cubs in the later developmental stage (approximately 5-19 months old) under varying social conditions. Laerke was temporarily co-housed with a wild-born, rescued grizzly bear cub (Jeb), affording both singleton cubs critical opportunities for socialization. Here, we focus on developmental trends in behavioral frequency and social proximity, as well as potentially influencing environmental factors. Our aim is to chronicle the similarities and differences between the two polar cubs, report on activity of the mother-reared cub, and describe the behavioral patterns observed during Laerke and Jeb's unique cross-species cohabitation period. For those accredited institutions continuing to breed and care for polar bears, such data as presented here provide preliminary baselines and check points against which to measure other individuals in the population or under similar rearing circumstances.

Methods

Ethics Statement

This study was reviewed and approved by the Detroit Zoological Society's (DZS) Animal Welfare and Management Committee and overseen by the Senior Director of Animal Welfare and Research.

Study Subjects and Location

The subjects of this study were two female polar bear cubs and one male grizzly bear cub residing at the Detroit Zoo in Royal Oak, Michigan, USA. The two polar bear cubs, Laerke and Astra, were born at the Detroit Zoo on November 17, 2020, to dam Suka and sire Nuka. Suka (approximately 8 years old in 2020) and Nuka (approximately 16 years old in 2020) had been residing at the Detroit Zoo since 2018 and 2011, respectively (Che-Castaldo & Meyerson, 2019). Although Suka gave birth to full-term litters in 2018 (single cub) and 2019 (twin cubs), this was her first litter to survive past the first week. She showed marked improvement in maternal care with each litter. Further information about Suka's maternal history has been published elsewhere (Gartland et al., 2023, 2024).

Suka initially reared both Astra and Laerke. On November 19, 2020 (i.e., two days postpartum), veterinary staff noted that Laerke appeared lethargic and weak. Additionally, Suka was observed rolling over onto Laerke. Veterinary and animal care staff deemed intervention medically necessary for Laerke's survival and removed Laerke from Suka's care. Astra remained with Suka while Laerke was hand-reared by expert staff in the Zoo's Ruth Roby Glancy Animal Health Complex. Hand-rearing was further necessitated when Laerke experienced four seizure episodes of unknown origin at around four months of age (March 16-18, 2021). Her seizures were treated with daily oral doses of phenobarbital (targeting 1 mg per kg, last dose administered February 28, 2022) and prednisone (20-30 ug/mL circulating in serum, last dose administered July 1, 2021), though no further seizure activity was observed after the first episodes (Bovee et al., 2025). Further details about Laerke's medical and rearing circumstances can be found in previous publications (Bovee et al., 2025; Gartland et al., 2024; Gartland et al., 2023). Efforts to reintroduce Laerke to Suka and Astra following Laerke's medical stabilization were not successful as Suka no longer appeared to recognize Laerke as her cub and reacted defensively when Laerke was in proximity to Astra.

Laerke transitioned from living at the Ruth Roby Glancy Animal Health Complex to living full-time at the Arctic Ring of Life (ARL) at approximately 4.5 months old. The ARL consists of both a behind-the-scenes indoor habitat space as well as two separate outdoor habitat spaces (Figure 1). Each of the outdoor habitat spaces measures approximately 3,066 m^2. The Pack Ice side of the habitat is equipped with gunite substrate, a stream, a 719,228 L saltwater pool, and a dry moat measuring approximately 3.66 m deep by 5.49 m wide. The Tundra side of the habitat is equipped with natural substrate, a 151,416 L freshwater pool, a cave, and a dry moat measuring approximately 3.66 m deep by 5.49 m wide. The behind-the-scenes indoor habitat space has a total animal space of approximately 144.4 m^2. This space is divided between seven dry stalls, a pool stall, the maternal den, two transfers, and a back hallway along the seven dry stalls. A detailed figure of this space has been previously published elsewhere (Gartland et al., 2024).

Laerke had access to the outdoor Tundra side of the ARL habitat (Figure 1) for the first time on April 20, 2021 at about 5 months old. Suka and Astra were given access to the outdoor Tundra side of the ARL habitat for the first time on April 26, 2021. Exactly which areas of the indoor habitat that the bears had access to rotated regularly based on outdoor habitat access and other management factors. However, housing proximity allowed all the bears to have visual, auditory, and olfactory access to each other, even during periods when Laerke was solitarily housed. Additionally, staff implemented protected contact with Laerke starting on June 18, 2021 (aged 31 weeks) for the safety of both Laerke and the care team.

Figure 1

Aerial View of the Outdoor Habitats at the Detroit Zoo's Arctic Ring of Life

The male grizzly bear cub, Jeb, was born in the wild in the general area of Tok, Alaska, USA. He was reported to be wandering alone around the town of Tok for multiple days. He was captured on June 9, 2021 by the Alaska Department of Fish and Game and transferred to the Alaska Zoo for temporary holding. Post-capture examinations estimated his date of birth to be mid-January 2021, making him approximately two months younger than Astra and Laerke. He was transferred to the Detroit Zoo on July 16, 2021, with the intention of socially housing him at the ARL with Laerke. Initial social introductions between Laerke and Jeb took place behind-the-scenes starting on August 1, 2021. The duo made their public debut on September 23, 2021 and remained socially housed until March 18, 2022. For Laerke and Jeb, social housing consisted of several hours of full physical access each day and overnight separation with mesh access. As their co-housing period drew to an end, their daily social time gradually decreased.

Dietary composition and portion size differed slightly between individuals and over time as individual nutritional needs shifted. At his arrival at the Detroit Zoo, Jeb received Esbilac formula (© Pet-Ag, Inc.), produce, herring, Nebraska meat, and Exclusive Lamb and Rice dog kibble (©Land O'Lakes, Inc.). Jeb was weaned off the Esbilac formula in January 2022. In addition to nursing from Suka, Astra also received herring, salmon oil, Nebraska meat, Exclusive Lamb and Rice dog kibble, produce, lard, and bones. Laerke received the same diet as Astra, with the addition of Esbilac formula until she was weaned in May 2022. Regardless of social housing condition, Laerke and Jeb were fed separately.

At the time of this study, the bears were managed in three units – (a) Suka and Astra, (b) Laerke and Jeb (following Jeb's arrival at the Detroit Zoo), and (c) Nuka. The units had rotating access to the behind-the-scenes and outdoor habitat spaces at the ARL (Figure 1). While the units had visual, auditory, and olfactory access to each other, no physical introductions took place during this study aside from those between Laerke and Jeb. With three units, this meant that one unit was always behind-the-scenes and thus not visible to observers. Originally, Nuka lived on the Pack Ice side of the ARL habitat while the other two units rotated access to the Tundra habitat. Starting on August 12, 2021, Suka and Astra were transitioned to the Pack Ice habitat, and the other two units rotated access to the Tundra side of the outdoor habitat. In practice, this rotation was not always as regular as intended, which impacted observation feasibility (Table 2). On February 8, 2022, Nuka was transferred to the Toledo Zoo on a breeding recommendation. After this transfer, Suka and Astra had primary access to the Pack Ice habitat while Laerke and Jeb had primary access to the Tundra habitat. On occasion, if Suka and Astra willingly shifted, the two units might switch between habitats for short periods. Following Laerke and Jeb's separation, the Zoo returned to having three units of bears rotating between the behind-the-scenes and outdoor ARL habitats.

Data Collection

Behavioral data were collected via live monitoring of the bears in their outdoor habitat utilizing 15 min focal follows with 1 min interval sampling of behavior, social proximity, substrate (land, water, indoors, unclear) and location, along with all-occurrence sampling of select behaviors. All data were recorded according to a pre-determined ethogram (Table 1). A total of four observers collected data, all of whom maintained a minimum inter-observer reliability rating of 90% with retesting at three-month intervals. Observers also recorded the date, time, temperature, weather condition, and crowd size at the start of each observation. Data collection took place once per day between 10 a.m. to 12 p.m., Monday through Friday, assuming bears were visible in their outdoor habitat.

Table 1

Behavioral Ethogram Used with Polar Bear and Grizzly Bear Cubs

Category	Behavior	Description
Behavior	Swim *	Cub interacts with pool when pool contains some amount of water. Swimming is locomotion within the water. Includes wading in water if water is not deep enough for full submersion.
	Nursing	Astra is actively drinking milk from Suka. This behavior is not applicable to Laerke or Jeb.
	Eating Solid Food	Cub is chewing, licking, or otherwise ingesting a non-milk/formula food.
	Drinking	Cub drinks water. This does NOT include nursing from Suka.
	Undesirable *	Focal is engaged in a repetitive behavior with no apparent purpose or an undesirable behavior for the species. Listed behaviors may include suckling, consuming non-food items, pacing, or head-swinging.
	Social Positive *	Cub is directing affiliative attention and behavior towards another individual (Suka or keeper/veterinary staff). This includes grooming, play behavior, and positive contact.
	Social Negative/ Correction *	Cub is directing aggressive or ill-mannered attention and behavior towards another individual (Suka or keeper/veterinary staff). This includes biting, swatting, and growling. Also score if Suka or keeper staff offers a correction (vocal, roll-away, etc.).
	Scratch/Self-Groom	Cub itches themself either with a paw or by rubbing their body against a wall or other structure in the environment. Should also include self-directed grooming behavior like licking, picking, or scratching.
	Object Interaction/Play	Cub investigates, plays with, or otherwise focuses attention on an enrichment object such as a boomer ball.
	Investigate	Cub sniffs, paws at, or otherwise examines aspects of their environment NOT including enrichment objects in a non-play centered manner. This can include examination of substrates, natural structures, plant life, or other habitat features.
	Solitary Play	Cub is amusing themselves without engaging with an object or participation from or interaction with Suka or keeper/veterinary staff. May include rolling around or zoomies.
	Vocalization	Cub emits a whine, growl, chortle, or other recognizable sound.
	Locomotion	Cub walks, runs, crawls, climbs or otherwise transports themselves from one location to another. Please note manner of locomotion.
	Excretion	Cub urinates or defecates.
	Alert	Cub is stationary, but alert and awake. Cub may be taking a break from another activity but still engaging with environment by looking around or sniffing.
	Resting	Cub is resting or sleeping, very little body movement, eyes are likely closed.
	Other	Cub is engaged in a behavior that does not fall under any of the previously outlined categories.
	Not Visible	Cub is obscured by structures/items in habitat (or by Suka) such that behavior cannot be reliably identified.
Social Proximity	Contact	Cub is in contact with social partner.
	< 1 m	Cub is less than 1 m from social partner.
	< 5 m	Cub is less than 5 m from social partner.
	> 5 m	Cub is more than 5 m from social partner.

Note. Behaviors marked with an * were also recorded on an all-occurrence basis. Ethogram is arranged according to priority of behaviors.

Data collection began when the polar bear cubs first had access to the outdoor habitat at approximately 23 weeks old. Although Laerke first had access to the Tundra habitat on April 20, 2021, data collection did not begin until two days later (April 22, 2021), while data collection for Astra began on April 26, 2021. Data collection for Jeb the grizzly bear cub began in August 2021 (approximately 32 weeks of age) after his arrival at the Detroit Zoo and successful introduction to Laerke. Given Laerke's shifting social housing conditions, including the period of protected contact, her social proximity could not always be scored. From June 18 until her August 18 introductions with Jeb (ages 31-40 weeks), Laerke did not have access to a social partner or the ability to be within social proximity to another individual during observations. Data collection for all three cubs ended in June 2022 when the polar bear cubs were approximately 19 months old. Across the entirety of the study period, we collected 119 hours of data (n = 470 observations) (Table 2). For most months of the observation period, there were between 21 and 23 total possible observation days per bear. The housing conditions discussed above impacted consistency of visibility and ability to collect data, particularly for Laerke and Jeb.

Table 2

Summary of Data Collected for Each Individual by Month and Year

Year	Age Range & Social Condition	Months	Astra		Laerke		Jeb	
			Total Hours	Total Observations	Total Hours	Total Observations	Total Hours	Total Observations
2021	5-8 months 23-37 weeks Laerke Solitary	April – July	11.75	47	15.75	57	-	-
2021	9-12 months 38-54 weeks Laerke with Jeb	August – November	19.25	77	6.25	25	4.50	18
2021-2022	13-16 months 55-71 weeks Laerke with Jeb	December – March	17.75	71	9.00	36	7.75	31
2022	17-19 months 72-85 weeks Laerke/Jeb Solitary	April – June	14.25	57	5.00	20	6.75	31
Total			63	252	36	138	20	80

Data Analysis

All inferential statistical analyses described in the following text were conducted using SAS©, 9.4.1 (Cary, NC, USA). Given the span of time over which observations occurred, as well as the myriad potential behavioral shifts occurring during seasonal and developmental transitions, descriptive data were largely presented in four-month periods (Table 2). These periods were based on the age of the polar bears and do not exactly align to Jeb's age. Jeb's age is clarified in figure titles where applicable. The delineation between 16 and 17 months for the last two periods was made on the basis of Laerke and Jeb's social separation to allow for comparisons surrounding that transition.

The three individuals experienced unique environmental conditions. As such, we elected to perform all analyses and report all results on an individual basis. Due to the small sample size, we primarily ran descriptive statistics corrected for visible time (mean and standard error) for visualization purposes. Due to the infrequency and short duration of Laerke and Jeb's time on the Pack Ice side of the habitat, this variable could not be individually investigated in analysis. Although not quite multicollinear, crowd size and temperature are closely related ($r = 0.37$, $n = 252$, $p < .001$), which presented some complications in teasing apart the effects of these two variables on behavior.

We used generalized linear mixed models (GLMMs) to examine the influence of environmental variables (weather condition, crowd size, and temperature) on counts of all-occurrence and interval behaviors as well as proximity patterns. Each model was run with a negative binomial distribution, a log link function, the log of the total visible intervals per observation as an offset variable, and the individual's age in months as the random intercept. We added an additional Newton-Raphson ridging optimization technique and a maximum iteration limit of 100 to better account for the over-dispersed dataset. Initial models included weather condition (Overcast, Partly Cloudy, Precipitation, Sunny), crowd size, and temperature as predictor variables. Final reported models include only significant independent variables and the intercept. However, in some cases, a predictor variable or the intercept was only significant when a non-significant predictor variable was retained in the model.

We used parameter estimates and associated t-tests to assess directional effects and categorical differences. To ensure robusticity of results, some behaviors were combined into single variables following methodology previously utilized with data on these individuals (Gartland et al., 2024). The behaviors "Nursing," "Drinking," and "Eating Solid Food" were combined into the single behavior of "Feeding." The behaviors "Object Interaction/Play" and "Solitary Play" were combined into the single behavior "Independent Play." The behaviors "Alert" and "Resting" were combined into the single behavior "Inactive." Additionally, behaviors that were only sparsely observed (comprising less than 1% of total activity budget adjusted for visibility) were excluded from GLMM analyses. This included interval data for "Scratch/Self Groom," "Social Negative," and "Other" behaviors for all three cubs. Additionally, all-occurrence data for "Undesirable," and interval occurrences of "Undesirable" and "Vocalization" were eliminated for Astra and Jeb due to infrequency. All data collected throughout the study are included in Astra's GLMMs. As Laerke and Jeb were socially housed for the majority (but not the entirety) of their data collection periods, GLMMs for these two individuals are restricted to data collected during social housing (ages 9-16 months for Laerke and ages 7-14 months for Jeb). For Laerke and Jeb, we cannot say whether a significant intercept represents change due to increasing age or change over the duration of the social housing period.

There were some cases in which a linear relationship predicted from visual representations of the data was reversed according to the GLMM results. This was particularly the case in models where the best fit model was trimmed to only include the random intercept as a predictor. We hypothesize that this reversal of relationships may have been due to Simpson's paradox (Simpson, 1951), a special case of ecological fallacy (Pollet et al., 2015). Simpson's paradox reverses the direction of a relationship within individual groups as a consequence of conducting a population-level analysis. This is most often seen when individuals are used as the random intercept, but would operate the same with our intercept of months given that the month creates the variation within the population of an individual's data. Behavioral data analyses may be particularly susceptible to Simpson's paradox given the tendency for sample data to be aggregated to a single score. In cases where we suspected Simpson's paradox to be impacting GLMM results for a model where the random intercept was the only retained predictor, we ran an additional Spearman correlation to contextualize the linear relationship between the given behavior and age in months.

Finally, we used Wilcoxon two-sample tests with a Monte Carlo sampling method at 10,000 permutations to examine significant variation between Astra and Laerke during Laerke's co-housing period, and variation in Jeb and Laerke's behavior between social housing conditions (socially housed together and individually housed). Behavioral categories were combined for analysis following the same guidelines as described for the GLMMs. Using a Monte Carlo sampling method to generate the test statistic corrects for potential statistical errors when conducting inferential statistics with small sample sizes (Plowman, 2008). In general, we conducted inferential analyses to determine when behavioral changes were statistically meaningful, rather than to extrapolate population level trends from data on these individuals.

Results

Astra

Astra's GLMMs suggest that as Astra aged, she decreased her percent of time spent in feeding, social positive, independent play, investigative, and inactive behaviors (Figure 2, Figure 3, Table 3). For each behavior, the random intercept (age in months) was the strongest or only significant predictor. In the case of feeding behaviors, this relationship may have been strongly influenced by the inclusion of nursing, as this behavior dropped precipitously between 6 and 10 months old while eating solid foods increased steadily between 13 and 19 months old (Figure 2, Figure 3). We suspected, based on Figure 2, that the GLMM for inactivity may have been subject to Simpson's paradox. This was preliminarily confirmed by a follow up Spearman correlation which demonstrated a significant positive relationship between Astra's age in months and her time spent in inactive behaviors ($r = 0.22$, $N = 252$, $p < .001$). While independent play declined with age, we saw more sustained object play compared to the more notable decrease in solitary or locomotory play (Figure 2).

Figure 2

(a-b) Percent of Visible Time Spent in Interval Behaviors and (c) Average Hourly Rate of All-occurrence Behaviors for Astra by Data Period

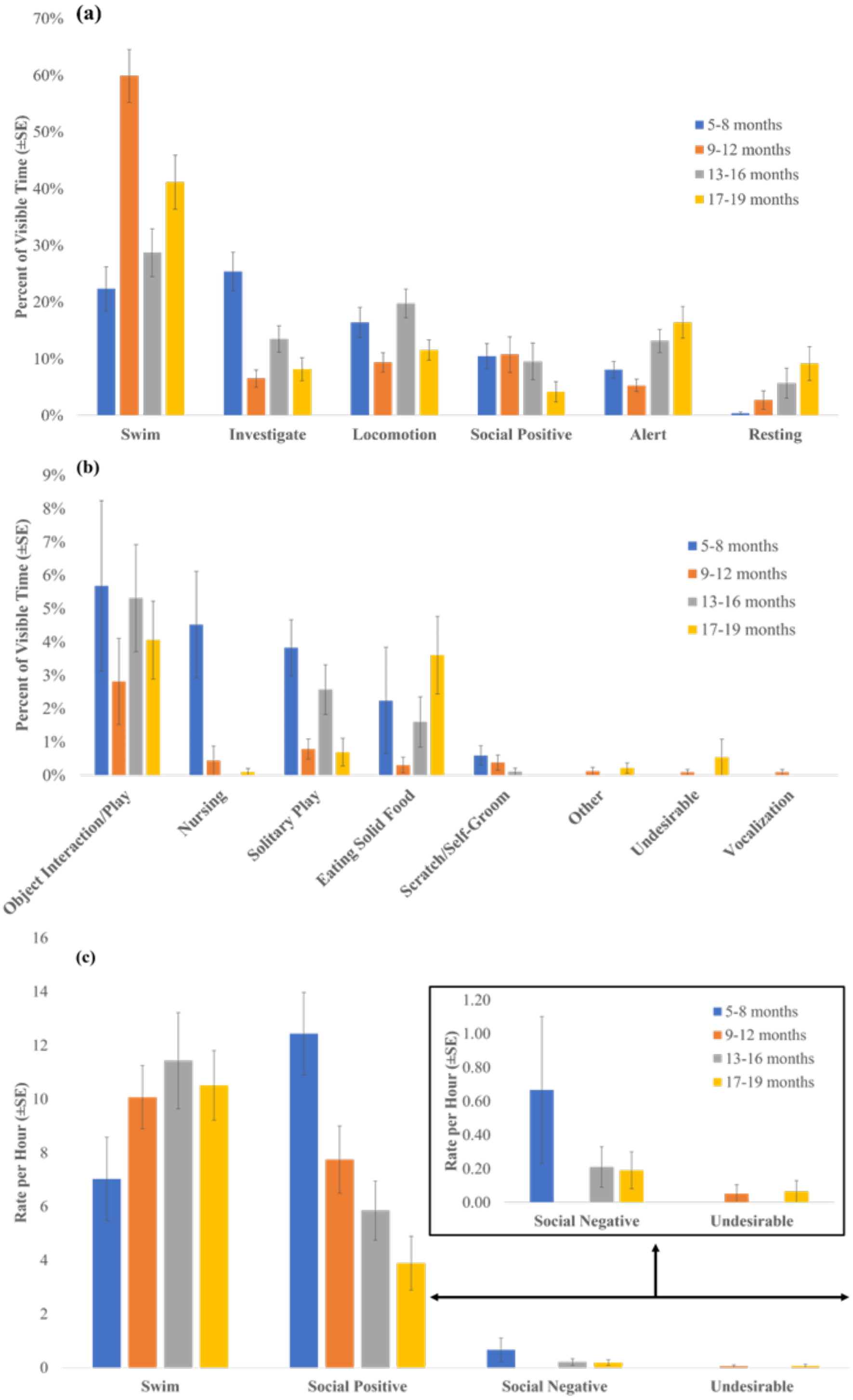


Table 3

Generalized Linear Mixed Models Examining the Influence of Age and Environmental Variables (Temperature, Weather Condition, and Crowd Size) on Behavior and Social Proximity for All Three Bears

Outcome Variable	Predictor	Est.	SE	DF	t	Pr >|t|	Lower	Upper
Astra								
Feeding	Intercept ***	-3.01	0.39	14	-7.65	<.0001	-3.86	-2.17
	Crowd Size *	0.34	0.15	236	2.36	.02	0.06	0.63
Social Positive	Intercept *	-0.80	0.35	14	-2.27	.04	-1.55	-0.04
	Weather – Overcast *	-0.90	0.45	235	-2.01	.05	-1.78	-0.02
Independent Play	Intercept ***	-1.35	0.15	14	-9.17	<.0001	-1.67	-1.03
Investigate	Intercept **	-0.76	0.18	14	-4.32	<.001	-1.13	-0.38
Swimming	Intercept	-0.74	0.49	14	-1.51	.15	-1.78	0.31
	Temperature **	0.02	0.01	234	2.96	<.01	0.01	0.04
	Weather – Overcast *	-0.39	0.19	234	-2.07	.04	-0.76	-0.02
	Weather – Partly Cloudy *	-0.35	0.17	234	-1.99	.05	-0.69	-0.01
	Weather – Precipitation	-0.47	0.28	234	-1.69	.09	-1.02	0.08
Locomotion	Intercept	0.12	0.29	14	0.41	.69	-0.51	0.75
	Temperature **	-0.01	0.01	237	-2.67	.01	-0.02	-0.003
Inactive	Intercept **	-0.62	0.19	14	-3.27	.0056	-1.03	-0.21
Hourly Rate of Swimming	Intercept	-0.21	0.19	14	-1.10	.28	-0.61	0.20
	Weather – Overcast	-0.37	0.20	235	-1.83	.07	-0.76	0.03
Hourly Rate of Social Positive	Intercept	-0.37	0.20	14	-1.85	.09	-0.80	0.06
	Weather – Overcast **	-0.85	0.24	235	-3.56	<.001	-1.32	-0.38
Hourly Rate of Social Negative	Intercept ***	-4.23	0.40	14	-10.70	<.0001	-5.08	-3.38
Hourly Rate of Undesirable	Intercept ***	-6.00	0.71	14	-8.44	<.0001	-7.49	-4.45
Contact	Intercept	-0.20	0.25	14	-0.82	.43	-0.74	0.33
	Weather – Overcast **	-0.82	0.31	235	-2.65	<.01	-1.43	-0.21
Within 1 Meter	Intercept **	-1.21	0.32	14	-3.79	<.01	-1.90	-0.53
	Temperature **	0.02	0.01	237	276	<.01	0.00	0.03
Within 5 Meters	Intercept **	-0.59	0.16	14	-3.77	<.01	-0.92	-0.25
	Weather – Partly Cloudy **	0.50	0.19	235	2.58	.01	0.12	0.88
More than 5 Meters	Intercept **	0.60	0.14	14	4.31	<0.001	0.30	0.89
Laerke								
Undesirable	Intercept **	-3.53	0.56	8	-6.32	<.001	-4.82	-2.24
Social Positive	Intercept **	-1.45	0.25	8	-5.85	<.001	-2.02	-0.88
Independent Play	Intercept *	-1.32	0.43	8	-3.05	.02	-2.31	-0.32
	Crowd Size *	-0.78	0.35	43	-2.24	.03	-1.49	-0.08
Investigate	Intercept *	-0.66	0.26	8	-2.55	.03	-1.25	-0.06
	Crowd Size	-0.27	0.15	43	-1.85	.07	-0.57	0.02
Swimming	Intercept **	0.71	0.14	8	4.91	.001	0.38	1.04
Vocalization	Intercept **	-2.59	0.48	8	-5.42	<.001	-3.69	-1.49
Locomotion	Intercept	0.15	0.33	8	0.45	.67	-0.61	0.91
	Temperature *	-0.01	0.01	43	-2.13	.04	-0.03	-0.001
Inactive	Intercept	-0.06	0.53	8	-0.11	.92	-1.29	1.17
	Temperature *	-0.02	0.01	43	-2.19	.03	-0.05	-0.002
Hourly Rate of Swimming	Intercept	0.56	0.30	8	1.87	.10	-0.13	1.25
	Temperature *	-0.02	0.01	42	-2.27	.03	-0.03	-0.002
	Crowd Size *	0.16	0.07	42	2.22	.03	0.01	0.31
Hourly Rate of Social Negative	Intercept	0.49	1.25	8	0.40	.70	-2.39	3.38
	Temperature *	-0.10	0.04	43	-2.43	.02	-0.18	-0.02
Hourly Rate of Undesirable	Intercept *	-11.02	4.02	8	-2.74	.03	-20.28	-1.75
	Temperature *	0.13	0.06	43	2.18	.04	0.01	0.25
Contact	Intercept **	-0.94	0.27	8	-3.41	.0092	-1.57	-0.30
Within 1 Meter	Intercept *	-0.81	0.28	8	-2.90	.02	-1.46	-0.17
More than 5 Meters	Intercept **	0.77	0.12	8	6.42	<.001	0.50	1.05
Jeb								
Feed	Intercept *	-2.95	1.24	7	-2.39	.05	-5.87	-0.03

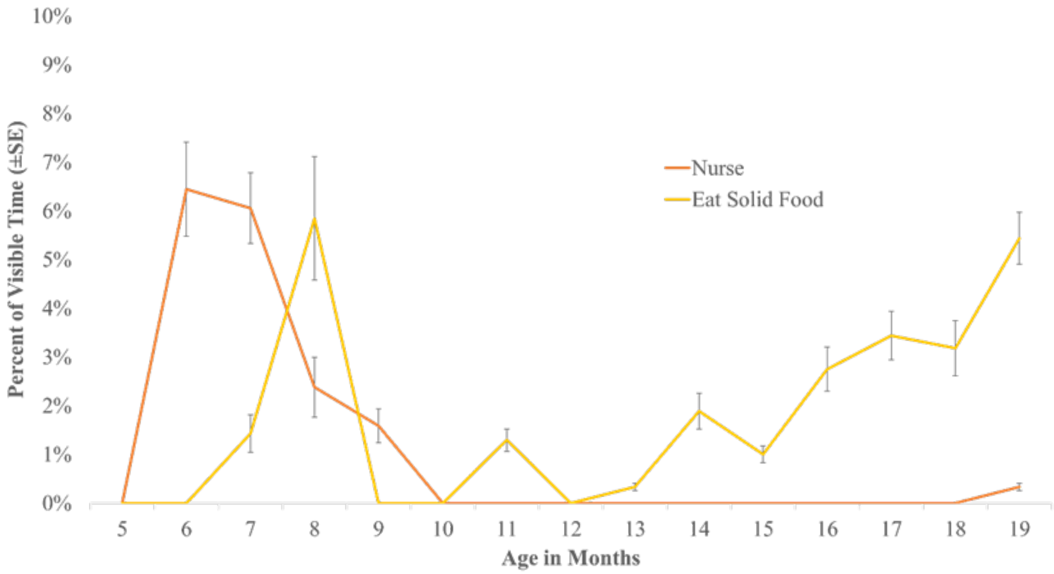
	Weather – Overcast	2.62	1.33	31	1.97	.06	-0.10	5.34
Social Positive	Intercept	-0.63	0.38	7	-1.66	.14	-1.53	0.27
	Weather – Overcast	-0.92	0.52	31	-1.75	.09	-1.99	0.15
	Weather – Partly Cloudy *	-1.05	0.51	31	-2.05	.05	-2.09	-0.01
Independent Play	Intercept **	-1.80	0.50	7	-3.61	<.01	-2.98	-0.62
Investigate	Intercept	0.72	0.34	7	2.14	.07	-0.07	1.52
	Temperature	-0.01	0.01	32	-1.79	.08	-0.03	0.002
	Crowd Size	0.08	0.08	32	1.00	.33	-0.08	0.24
Swim	Intercept **	-2.87	0.85	7	-3.37	.01	-4.89	-0.86
	Temperature **	0.05	0.02	33	3.16	<.01	0.02	0.09
Inactive	Intercept **	-1.17	0.20	7	-5.81	<.001	-1.65	-0.69
Hourly Rate of Swimming	Intercept *	-0.98	0.31	7	-3.17	.02	-1.71	-0.25
Hourly Rate of Social Positive	Intercept	0.68	0.32	7	2.17	.07	-0.06	1.43
	Weather – Overcast	-0.42	0.36	31	-1.16	.25	-1.16	0.32
	Weather – Partly Cloudy	-0.43	0.34	31	-1.27	.21	-1.12	0.26
	Weather – Precipitation	-0.57	0.52	31	-1.10	.28	-1.62	0.49
Hourly Rate of Social Negative	Intercept **	-3.05	0.45	7	-6.79	<.001	-4.11	-1.99
Contact	Intercept **	-1.02	0.21	7	-4.82	<.01	-1.52	-0.52
Within 1 Meter	Intercept **	-2.02	0.54	7	-3.76	<.01	-3.29	-0.75
	Weather – Overcast *	-0.73	0.36	30	-2.04	.05	-1.46	0.002
	Temperature **	0.04	0.01	30	4.21	<.001	0.02	0.05
Within 5 Meters	Intercept	-0.58	0.44	7	-1.34	.22	-1.61	0.45
	Weather – Overcast	0.28	0.31	30	0.90	.38	-0.36	0.92
	Weather – Partly Cloudy	-0.03	0.31	30	-0.09	.93	-0.66	0.60
	Weather – Precipitation	0.55	0.43	30	1.29	.21	-0.32	1.43
	Temperature *	0.01	0.01	30	2.25	.03	0.00	0.03
More than 5 Meters	Intercept *	1.11	0.37	7	2.96	.02	0.22	1.99

Note. Age (and co-housing duration, for Laerke and Jeb) is represented by the intercept in each model. The reference category for Weather was Sunny. Reported final models only included significant or trending weather categories, unless weather was retained for best fit. Behaviors that demonstrated no significant relationship to either the random intercept or predictor variables are not included in this table.
* indicates significance at $p \leq .05$. ** indicates significance at $p \leq .01$. *** indicates significance at $p \leq .0001$.

The relationship between social positive behaviors and age is tentatively supported by results for hourly rates of social behaviors, although hourly rate of social positive behavior only trended towards decreasing as Astra aged (Figure 4, Table 3). As both percent of time spent in and hourly rate of social positive behaviors were also significantly lower in overcast weather conditions (Table 3), weather may actually be the best predictor for social positive interactions between Suka and Astra. The same appears to be true for both swimming and locomotory behaviors, as time spent in locomotion significantly decreased in higher temperatures while time spent swimming increased in higher temperatures and decreased in overcast, partly cloudy, and precipitation conditions as compared to sunny conditions (Table 3). Although temperature had greater significance as a predictor for time spent swimming, weather conditions demonstrated considerably stronger effects as indicated by the parameter estimate (Table 3). The effect size of temperature on locomotion was also relatively weak (Table 3). Astra demonstrated a decreased hourly rate of undesirable behaviors (specifically pacing) as she aged (Table 3). However, this behavior was very infrequent and only observed in the periods surrounding Laerke and Jeb's introduction and eventual separation (Figure 2c).

Figure 3

Astra's Average Percent of Visible Time Spent Nursing and Eating Solid Food by Age (in Months)

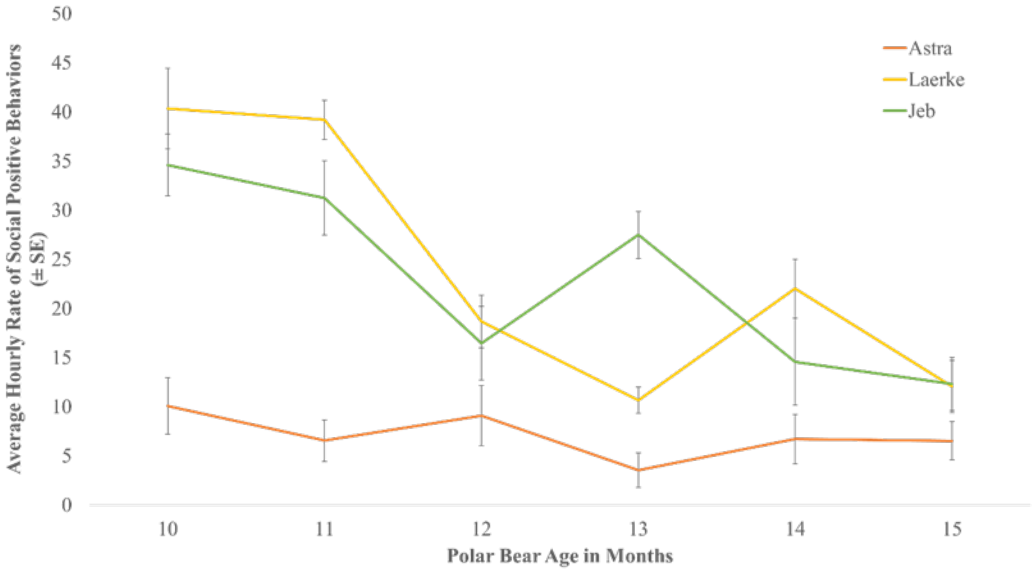


Note. This graph only presents the time period when all three bears had access to a social partner.

Feeding was the only behavior that showed a significant effect of crowd size, but the increase in feeding associated with larger crowds had a relatively weak effect size, particularly when compared to the effect of the random intercept (Table 3).

Figure 4

Hourly Rates of Social Positive Interactions by Month for Astra, Laerke, and Jeb

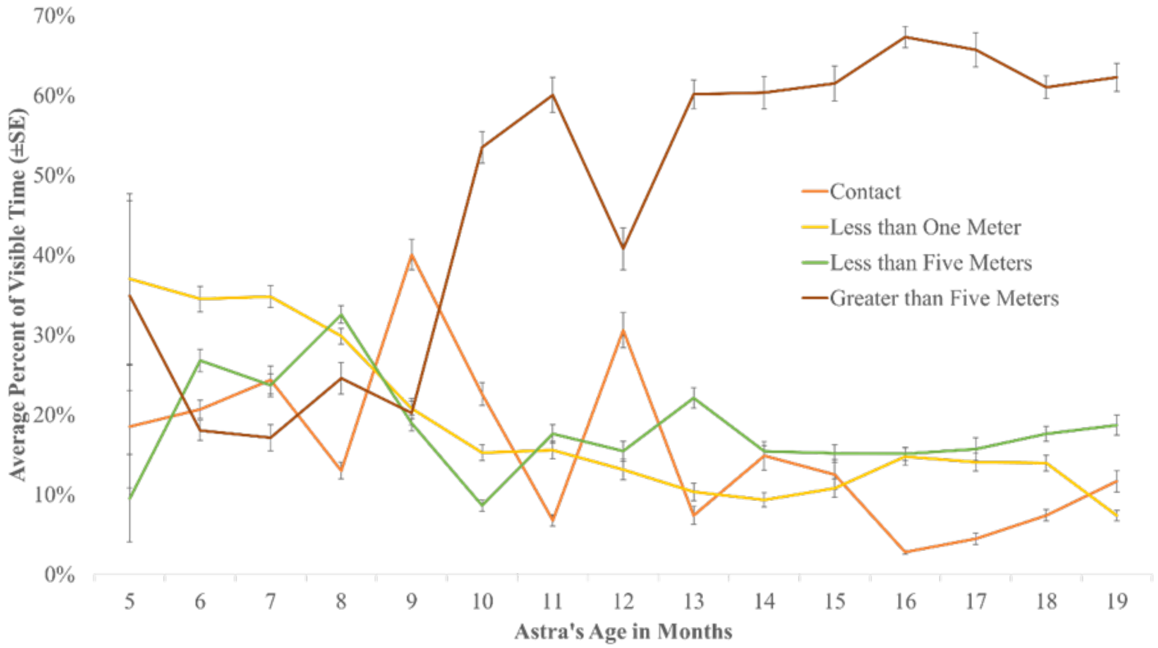


Note. This graph only presents the time period when all three bears had access to a social partner.

Similarly to swimming, Astra's time spent in contact with Suka was best predicted by weather conditions, with contact decreasing in overcast conditions (Table 3). However, Astra's time spent within one meter, within five meters, and at distances greater than five meters from Suka were best predicted by Astra's age (Figure 5, Table 3). While weather and temperature were also significant predictors of these proximity categories, the significance levels and effect sizes indicate lesser influence compared to age (Table 3). There may be inter-relatedness between observed patterns of social interactions, swimming, and proximity. Anecdotally, observers reported frequent bouts of positive or playful contact/proximity between Suka and Astra when both individuals were utilizing the pool. Astra's tendency to swim more in warmer, non-overcast conditions may have had a cascading effect on social behaviors and proximity patterns.

Figure 5

Astra's Proximity to Suka by Age (in Months)



Astra and Laerke Comparisons

From the approximate ages of 9-16 months, when both Astra and Laerke had access to social partners (Suka and Jeb, respectively), we saw no significant variation in percent of time spent in social behaviors or at different proximities to social partners (Table 4). Astra and Laerke demonstrated no significant variation in most monitored interval behaviors, apart from vocalization, feeding, and undesirable behaviors (Table 4). Although percent of time in social behaviors did not vary between individuals, we did find that Laerke had significantly higher all-occurrence social positive and social negative interactions than Astra (Table 4). Laerke also demonstrated significantly higher hourly rates of swimming and undesirable behaviors.

Table 4

Wilcoxon Two-sample with Monte Carlo Exact Test Results Comparing Astra and Laerke's Interval and All-occurrence Social Behaviors During Laerke's Co-housing Period

Behavior Type	Behavior	Average Rate or Percent of Time (Mean ± SE)		Statistic (S)	Z	Pr > |Z|	Pr > |S-Mean|
		Astra N=139	Laerke N=53				
All-Occurrence	Social Positive ***	6.91±0.84	20.43±2.38	6880.5	5.3213	<.0001	<.0001
	Social Negative **	0.09±0.05	0.79±0.36	5457.50	2.7208	.0065	.0034
	Swim **	10.72±1.02	15.20±1.68	6067.50	2.8008	.0025	.0045
	Undesirable **	0.03±0.03	0.62±0.28	5437.50	3.1132	.0009	.0025
Interval	Social Positive	10.20±2.23%	5.49±1.18%	5509.50	1.4475	.15	.15
	Social Negative	0.00±0.00%	0.16±0.16%	5184.00	1.6195	.11	.28
	Swim	45.97±3.40%	44.79±4.99%	5130.50	0.0473	.4811	.9620
	Feeding ***	1.23±0.44%	8.25±1.95%	6242.00	5.11	<.0001	<.0001
	Undesirable *	0.05±0.05%	0.77±0.41%	5367.00	2.6590	.0039	.0139
	Independent Play	5.54±1.09%	3.48±0.98%	4905.50	-0.6	.45	.45
	Investigation	9.64±1.37%	8.80±1.72%	5224.50	0.3526	.3622	.7243
	Vocalization ***	0.05±0.05%	2.36±-.83%	5647.50	4.2279	<.0001	<.0001
	Locomotion	13.97±1.52%	14.78±1.93%	5451.50	1.0056	.1573	.3159
	Inactive	12.81±1.84%	8.45±1.43%	5092.50	-0.07	.95	.95
	Contact with Social Partner	15.94±2.22%	10.47±1.66%	5257.50	0.4495	.65	.65
	<1 m from Social Partner	17.46±1.92%	11.79±1.96%	4880.50	-0.7092	.48	.48
	<5 m from Social Partner	18.64±1.80%	21.90±2.51%	5677.50	1.6570	.10	.10
	>5 m from Social Partner	47.95±3.27%	55.84±3.88%	5651.00	1.5652	.12	.12

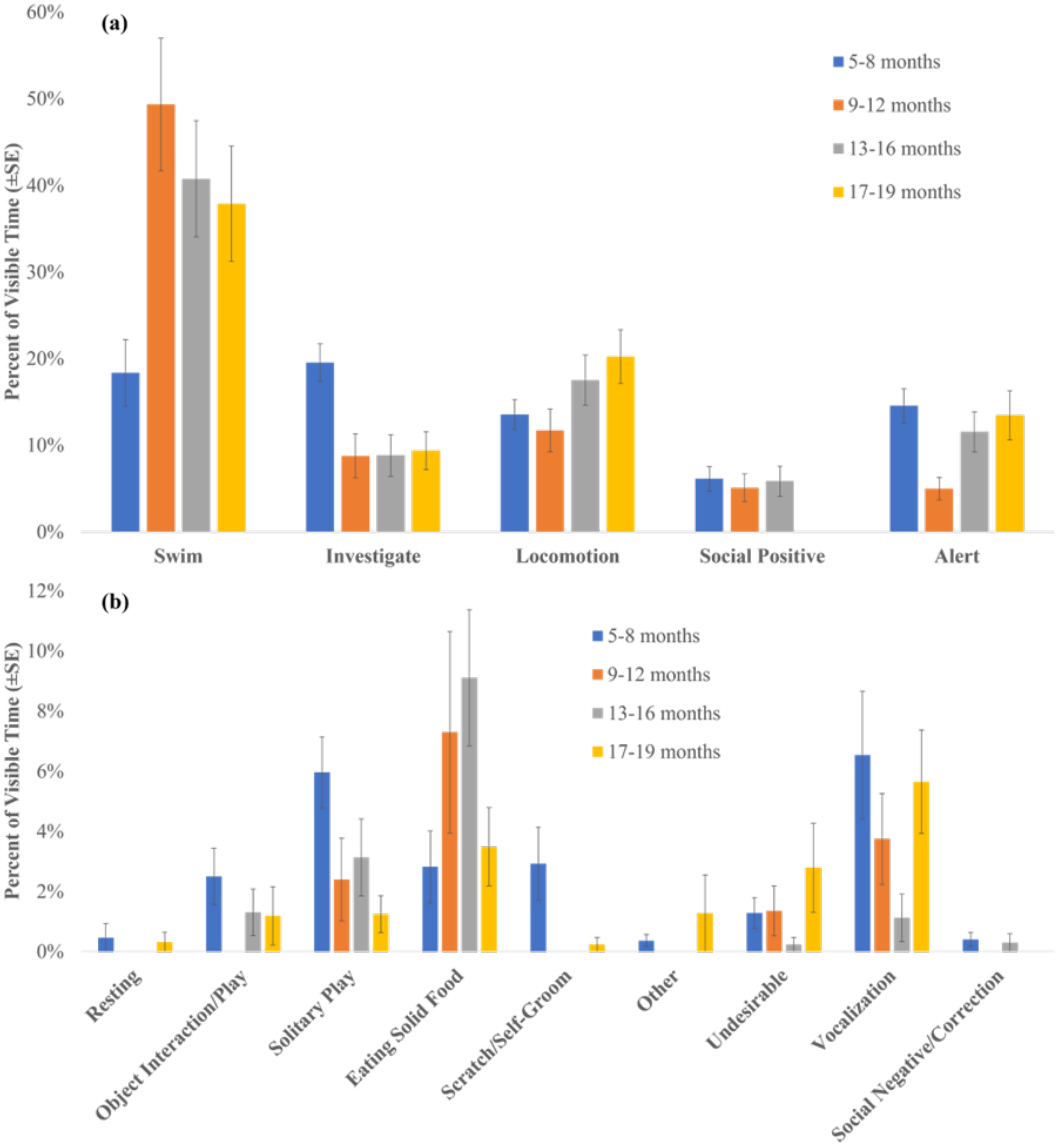
Note. * indicates significance at p ≤ .05. ** indicates significance at p ≤ .01. *** indicates significance at p ≤ .0001.

Laerke – Behavior Throughout the Social Housing Period

The GLMMs for Laerke were restricted to data collected when she was co-housed with Jeb, representing the periods from 9-12 and 13-16 months. Thus, we cannot say whether the random intercept measures individual age or duration of the social housing period. A total of three models (time spent feeding, time spent within five meters of Jeb, and hourly rate of social positive behaviors) demonstrated no trending or significant relationship with either the random intercept (age in months) or the predictor variables, but multiple behaviors were significantly predicted by the random intercept (Table 3). During the social housing period, Laerke's percent of time spent in undesirable, social positive, independent play, swimming, and vocalization behaviors, as well as her hourly rate of undesirable behaviors, were best predicted by the random intercept (Table 3). Each of these behaviors, aside from swimming, decreased as Laerke aged/over the duration of the social housing period, although this was only evident in the statistical analyses and is less apparent in the activity budgets when broken down into multi-month periods (Figure 6). Percent of time spent swimming increased throughout the social housing period (Table 3). Proximity measures demonstrated similar relationships with the duration of the social housing period (Figure 7). Specifically, Laerke decreased her time in contact with Jeb and within 1 m of Jeb and increased her time spent at distances of greater than 5 m from Jeb over the social housing period.

Figure 6

Activity Budget for Laerke by Data Period.



Note. Laerke was in solitary housing during the 5-8 month and 17–19-month periods and was co-housed with Jeb in the 9-12 month and 13–16-month periods.

Although the random intercept was the strongest predictor of many tested behaviors both in terms of significance and effect size, some behaviors were also or solely significantly influenced by temperature or crowd size (Table 3). Independent play and investigative behaviors decreased or trended towards decreasing in higher crowd size conditions, though to a lesser effect than the influence of the random intercept. Percent of time spent in locomotory and inactive behaviors as well as hourly rate of social negative behaviors were negatively influenced by temperature, with temperature being the sole significant predictor of both interval locomotion and all-occurrence social negative behaviors (Table 3). Additionally, while both percent of time and hourly rate of undesirable behaviors were most significantly predicted by the duration of the social housing condition, hourly rate or frequency also increased as temperatures increased although the effect size is almost negligible (Table 3).

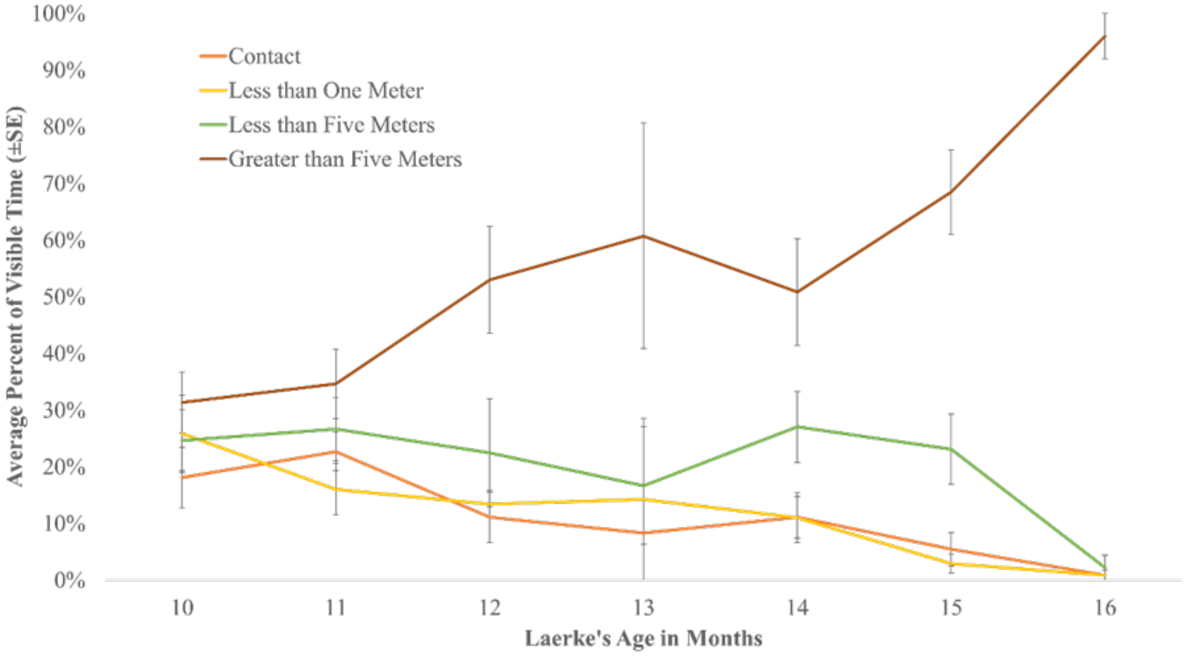
Of note is that while Laerke's percent of time spent in social positive interactions with Jeb decreased throughout the social housing period, we observed no effect of environment or housing duration on the hourly rate of social positive interactions (Table 3). Again, suspecting the potential of Simpson's paradox, we ran an additional Spearman correlation which demonstrated that rate of social positive interactions significantly decreased with duration of social housing ($r = -0.62$, $N = 43$, $p < .0001$). This suggests that both the frequency and duration of any given interaction decreased over time. Similarly, while percent of time spent swimming was best predicted by duration of the social housing condition, Laerke's hourly rate of swimming or the frequency with which she entered the pool was better predicted by temperature and particularly crowd size (Table 3).

Laerke – Contrasting Social and Solitary Housing Conditions

Following her separation from Jeb, Laerke demonstrated a significant decrease in all-occurrence swimming and a significant increase in percent of time spent vocalizing (Table 5). As social and proximity behaviors were no longer possible during solitary housing, we did not compare these behaviors between conditions.

Figure 7

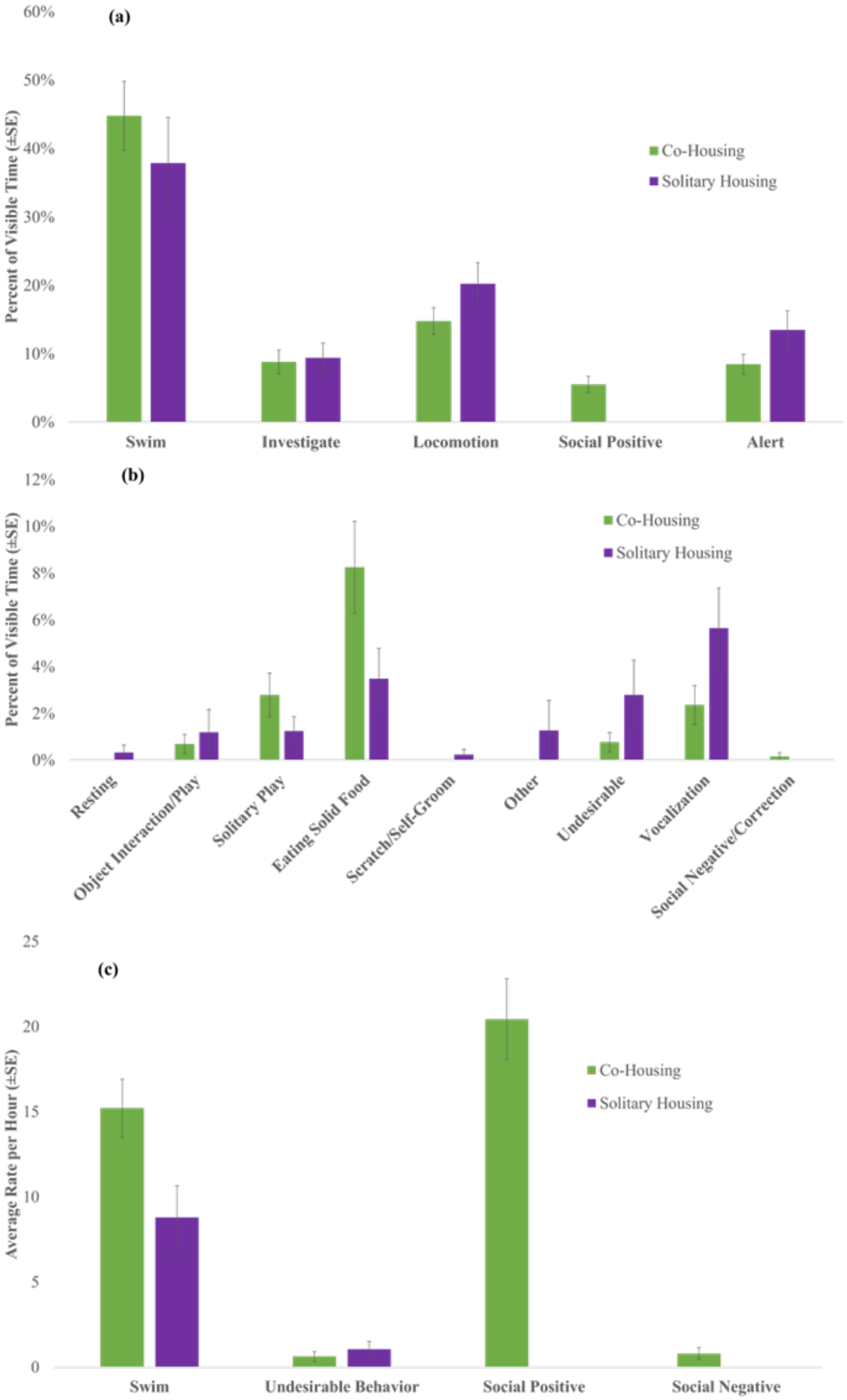
Laerke and Jeb's Proximity During the Co-housing Period



Although undesirable behavior decreased throughout the social housing period, we saw no significant difference in overall rates or overall percent of visible time spent in undesirable behaviors between when Laerke was co-housed with Jeb and when she was solitarily housed (Figure 8; Table 5). In fact, the vast majority of tested applicable behaviors demonstrated no variation between housing conditions.

Figure 8

(a-b) Laerke's Activity Budget and (c) Laerke's Hourly Rate of All-Occurrence Behaviors by Social Housing Condition



Note. Data in the co-housing condition represents the time period spanning the 9–16-month age period while data in the solitary housing condition represents the time period spanning the 17-19-month age period.

Jeb – Behavior Throughout the Social Housing Period

The model for locomotion demonstrated no trending or significant relationship with either the random intercept (age in months) or the predictor variables (Table 3). Jeb's behaviors were frequently influenced by weather and temperature conditions in addition to the random intercept (age and duration of social housing period) (Table 3). The observed hourly rate of swimming and social negative interactions decreased throughout the social housing period. Jeb was never recorded in either interval or all-occurrence undesirable behaviors during the social housing period (Figure 9). Jeb's percent of time spent in feeding, social positive, independent play, swimming, and inactive behaviors all decreased throughout the social housing period, as did his time spent in contact and within one meter of Laerke. However, percent of time spent in feeding, social positive, investigative, and swimming behaviors also demonstrated significant or trending relationships with temperature or weather. In many of these cases, the effect size (as demonstrated by the significance level and estimate) was notably lower than the effect of age. The exception to this is feeding behaviors, for which the positive effect of overcast weather was nearly equal to the negative effect of duration of the social housing period (Table 3). Similarly to Astra, Jeb's time spent swimming was positively influenced by the temperature, but the effect size was small and not nearly as significant as the effect of time.

Time spent in investigative behaviors and time spent at distances of more than five meters from Laerke were the only behaviors to demonstrate a significant positive relationship with time (Table 3). Although hourly rate of social positive interactions with Laerke also demonstrated this positive relationship with time according to the GLMMs, we again suspect Simpson's paradox. This is supported by the post-hoc Spearman correlation which indicates a significant negative relationship between these two measures ($r = -0.53$, $N = 40$, $p < 0.001$). Percent of time spent in social positive behaviors demonstrated no relationship with time, but a negative relationship with overcast and partly cloudy weather conditions. When paired with the results for the hourly rate of social positive behaviors, this suggests that Jeb may have engaged in decreasing frequency of interactions over time, but the duration of these interactions was governed by weather conditions more than duration of social housing.

Jeb – Contrasting Social and Solitary Housing Conditions

When comparing overall behavior across conditions, Jeb spent significantly more time inactive during the solitary housing period (Figure 9; Table 5). He also trended towards increasing both percent of time and hourly rate of undesirable behavior. Of note, this behavior was only recorded in the solitary housing condition and largely consisted of pacing along the border between habitats, particularly when another bear was visible. He trended towards decreasing time spent eating solid food and engaging in independent play during the solitary housing period as well (Figure 9; Table 5). He demonstrated no other significant behavioral shifts between social housing conditions (Figure 9; Table 5).

Table 5

Wilcoxon Two-Sample with Monte Carlo Exact Test Results Comparing Interval and All-Occurrence Behavior Between Social Housing Conditions for Laerke and Jeb

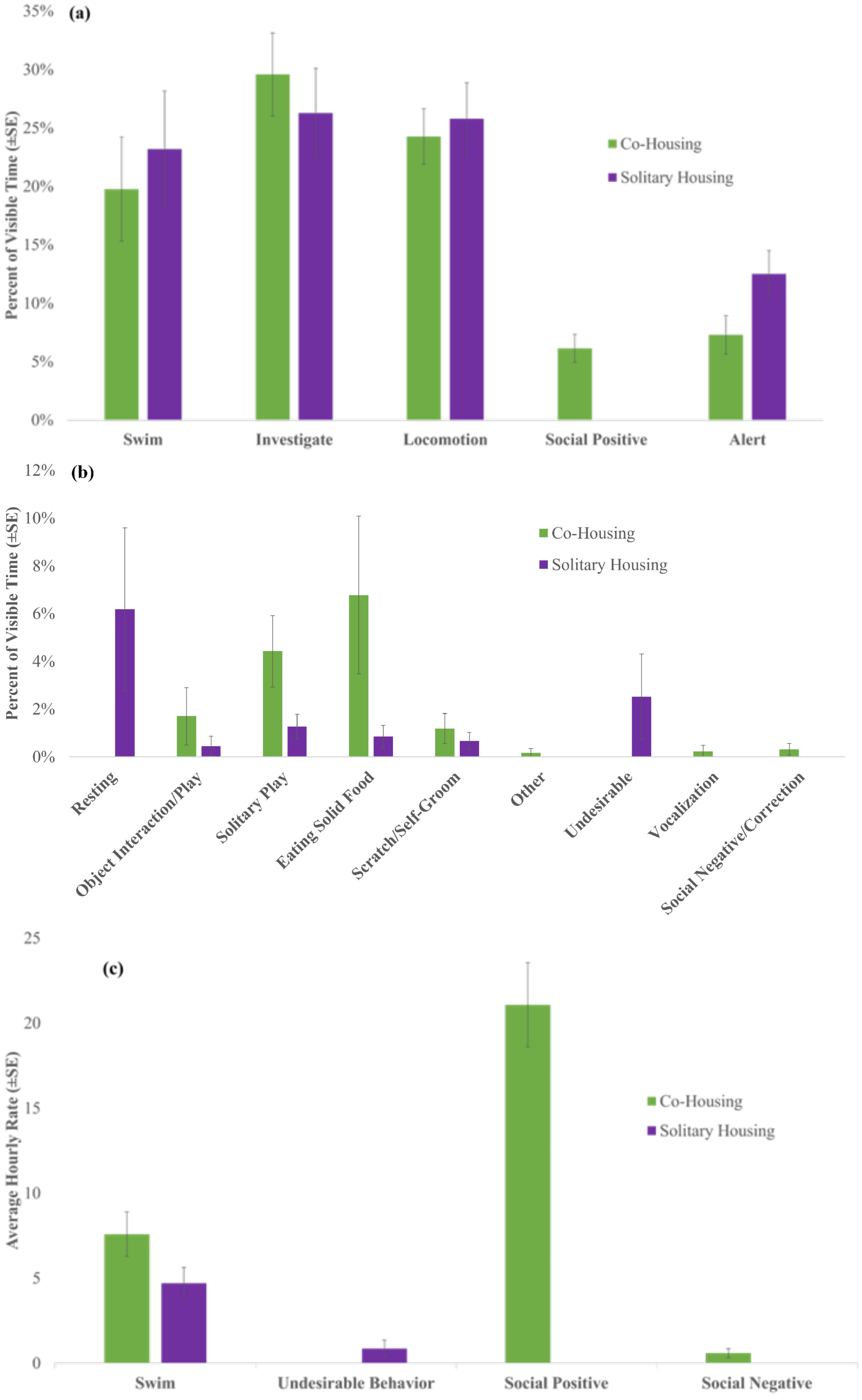
Behavior Type	Behavior	Statistic (S)	Z	Pr > |Z|	Pr > |S-Mean|
		Laerke			
All-Occurrence	Undesirable	1208	10429	.30	.36
	Swim **	890	-2.573	.01	.01
Interval	Eating Solid Food	1040	-1.279	.20	.20
	Undesirable	1202.5	1.0455	.30	.28
	Independent Play	1112.50	-0.47	.63	.62
	Investigation	1172.5	0.2640	.79	.80
	Swim	1064.5	-0.8370	.40	.41
	Vocalization **	1339	2.5068	.01	.01
	Locomotion	1281.5	1.3384	.18	.18
	Inactive	1304.50	1.60	.11	.11
	Other	1174.5	1.3758	.17	.35
		Jeb			
All-Occurrence	Undesirable	1563	1.8910	.06	.10
	Swim	1349.5	-1.4782	.14	.14
Interval	Eating Solid Food	1372.5	-1.8929	.06	.05
	Undesirable	1563	1.8909	.06	.10
	Independent Play	1359.50	-1.78	.08	.07
	Investigation	1410	-0.8567	.39	.39
	Swim	1485	-0.1418	.89	.89
	Vocalization	1480	-0.9276	.35	.00
	Locomotion	1494	-0.0386	.97	.97
	Inactive **	1758.00	2.61	.01	.01
	Other	1480	-0.9276	.35	1.00

Note. Data in the co-housing condition represents the time period spanning the 9 to 16-month age period for Laerke and the 7 to14-month age period for Jeb. Data in the solitary housing condition represents the time period spanning the 17 to19-month age period for Laerke and the 15 to17-month age period for Jeb.

* indicates significance at p ≤ .05. ** indicates significance at p ≤ .01.

Figure 9

(a-b) Jeb's Activity Budget and (c) Jeb's Hourly Rate of All-Occurrence Behaviors by Social Housing Condition



Note. Data in the co-housing condition represents the time period spanning the 7-14-month age period while data in the solitary housing condition represents the time period spanning the 15–17-month age period.

Discussion

Astra: Nursing and Feeding

Although the sample size presented here is very limited, these data do present preliminary opportunities for establishing relationships between behavior, age, and environment. Post-den emergence, Astra's nursing decreased with age (Gartland et al., 2024). This trend appeared to continue in her later development, supporting what has been observed in previous studies of lactation and milk consumption in polar bear cubs (Arnould & Ramsay, 1994; Derocher et al., 1993; Greenwald & Dabek, 2003). As cubs age, nursing bouts may decrease in frequency but increase in duration while time between maternal contacts increases (Greenwald & Dabek, 2003). However, of note is that Astra's actual time spent in contact with (not just proximate to) Suka did not change with time.

Previous studies of wild maternal groups have noted that the functional onset of weaning is poorly understood in this species, due in part to challenges in year-round direct observations (Martin, 1984; Polischuk et al., 2001). Wild polar bears will continue to nurse past the yearling stage, interspersed with foraging with their mother, leading to an unusually long lactation period as compared to other bear species (Arnould & Ramsay, 1994; Gittleman & Oftedal, 1987). Astra was still regularly nursing from Suka in the spring of her first year, as has been observed for wild cubs (Polischuk et al., 2001), but she had almost entirely ceased nursing by September 2021 at approximately ten months of age. Feeding (as representing the combination of nursing and consumption of solid foods) was negatively related to age. However, descriptive data showed that nursing and consumption of solid food over time demonstrated an inverse relationship. A number of factors may have contributed to the reported statistical results for feeding. It is possible that the novelty of Jeb's arrival and increased attention towards swimming behaviors in the August-November 2021 time period contributed to temporary decreases in feeding behaviors. Food abundance, lack of predation risk and hunting competition, and relative climate stability may also facilitate earlier weaning for zoo-born cubs than their wild-born counterparts.

Play Behavior

Ethological and evolutionary studies of play behavior generally agree that play peaks in mid-late infancy and again in the yearling period before generally decreasing as the individual reaches and advances into adulthood (Bekoff, 1972; Burghardt, 2005; Byers & Walker, 1995; Hill & Ramirez, 2014). Although play decreases in adulthood, play behaviors in wild polar bears may continue to be frequent in yearlings of both singleton and twin litters (Bissonnette, 2020; Hansson & Thomassen, 1983). In the case of Astra, we observed an initial emergence of solitary play behavior in infancy (eight weeks) (Gartland et al., 2023). This was sustained into the den-emergence period (Gartland et al., 2024) and continued after she transitioned to having more full-time access to the outdoor habitat before beginning to decrease at around nine months of age (August 2021). This decrease was most notable in locomotor forms of independent play, as we observed more sustained object play even after the nine-month mark, which may have implications for husbandry and enrichment planning. Laerke and Jeb, despite their very different environmental conditions, demonstrated similar patterns. We observed a strong negative relationship between all three bears' age in months and their engagement in independent play, supporting observations of the relationship between play and the advent of adulthood. However, accurate assessment of patterned play behavior is somewhat complicated by how swimming was defined in this study.

According to our ethogram, all behaviors observed while the individual was in significant contact with water were recorded as swimming. In practice, this included many interval behaviors that would otherwise have been recorded as independent play (enrichment-directed, diving, leaping) or social play. Given the potential obfuscation caused by the ethogram and methodology, it is unclear if Astra demonstrated any meaningful decrease in independent play behavior during the duration of this study. However, given that there was no relationship between either percent of time or hourly rate of swimming with age, it is likely fair to assume that the established relationship between play and age is valid despite these methodological limitations.

Swimming Behavior

In wild polar bears, swimming primarily serves a locomotory function (Pagano et al.,2012). Although polar bears of all age and sex classes are renowned swimmers, subadults and cubs swim at higher rates than adults (Stirling, 1990). The captive cub studied by Greenwald and Dabek (2003) increased the proportion of time spent swimming from ages four to seven months, though this may have been influenced by rising temperatures. Swimming bouts during this time tended to be shorter in duration but high in frequency, and interspersed with time on land and contact with the mother (Greenwald & Dabek, 2003). Swimming duration for Astra peaked in September. Observers also anecdotally noted an increase in frequency and duration of maternal contact during pool use. This represents an opposing trend to that observed by Greenwald & Dabek (2003), though as both studies are case studies of single individuals, it is not possible to establish which developmental trend may be applicable at a population level. We observed a similar relationship between temperature and weather conditions in Astra and Jeb's swimming behaviors, though Laerke's swimming was more strongly influenced by duration of the social housing period. For Laerke, time spent swimming increased throughout the social housing period, but frequency decreased following her transition to solitary housing. Anecdotally, observers reported that Jeb did not enter the pool as readily as Laerke, particularly in lower temperatures. Given the increased frequency and roughness of play initiated by Jeb throughout the social housing period, we suspect that Laerke may have been using the pool as a way to avoid social interactions. Specific details as to the quality and frequency of social play between Laerke and Jeb are discussed later.

Astra: Independence and Maternal Separation

It is difficult to judge the appropriate timing of maternal independence in zoo-reared cubs. Previous studies of brown bears have noted that human proximity may result in extended maternal care (Van de Walle et al., 2019). We observed a significant decrease in Astra's social proximity to Suka beginning in September 2021 (ten months old) and extending through cessation of monitoring at 19 months. We saw similar gradual declines in social positive interactions, with rates of interactions declining from an average of 20 instances per hour in April 2021 (6 months old) to less than 5 instances per hour in June 2022 (19 months old). Astra's behavioral pattern follows established trends for independence at between one and two and a half years old observed in wild populations (Derocher & Stirling, 1995; Furnell & Schweinsburg, 1984; Hansson & Thomassen, 1983; Kistchinski & Uspenski, 1972; Larsen, 1985; Lentfer & Hensel, 1980; Lønø, 1970; Ramsay & Stirling, 2009). This pattern of decreased nursing and increased independence continues the trend observed by other studies of the early neonate and den emergence developmental periods (Gartland et al., 2024; Gartland et al., 2023; Greenwald & Dabek, 2003).

Astra and Laerke: Developmental Comparison

Given her more typical mother-rearing environment, Astra at times served as a control against which to compare Laerke's behavioral development, as well as a basis for assessing the social relationship between Laerke and Jeb. Previously observed similarities in the activity patterns and adrenal activity between Astra and Laerke (Gartland et al., 2024; Bovee et al., 2025) were hypothesized to result from a combination of canalization (Lickliter & Harshaw, 2010; Waddington, 1942) and intentional management decisions. Both Astra and Laerke decreased time spent in independent play and investigatory behaviors as they aged. When both cubs had access to social partners, Astra and Laerke did not differ in their time spent in key behaviors including swimming, investigation, independent play, locomotion, and inactive behaviors. They also demonstrated similar proximity patterns. These results continue the observed similarities in activity patterns previously observed between these two individuals (Gartland et al., 2024). The observed variations in time spent vocalizing, feeding, and engaging in undesirable behaviors can likely be explained by environmental and husbandry differences between the individuals. For example, Laerke was not nursing, so her sole source of food was solid dietary items, likely explaining the greater time spent eating solid food. Ultimately, these results support Laerke's ability to develop normally, likely assisted by her social housing period with Jeb, as assessed by her similarities to Astra.

We saw more marked differences in hourly rates of all-occurrence behaviors such that Laerke demonstrated more frequent episodes of social positive, social negative, swimming, and undesirable behaviors. Astra's undesirable behavior consisted of limited pacing along the Pack Ice-Tundra habitat border. This occurred for a brief period when Jeb was introduced to Laerke and first had access to the Tundra habitat, and again when Laerke and Jeb were later separated and Jeb had solo access to the Tundra habitat. The relationship between Astra's age and rate of undesirable behavior, although statistically meaningful, is less likely to be biologically meaningful. Laerke's undesirable behaviors consisted of suckling on inappropriate items (e.g., habitat surfaces, her own paw, the air), consumption of non-diet food items (dirt and grass), and pacing. On habitat during observations, consumption of non-diet food items was the most frequently reported undesirable behavior. However, animal care staff reported frequent observations of suckling when Laerke was housed behind the scenes. In the case of the suckling behavior, we hypothesize that this may stem from Laerke's hand-rearing environment, as she did not have an appropriate item (a teat) available for suckling and comfort seeking like Astra. Similarly, Laerke was housed with another juvenile individual, while Astra was housed with an adult, which may have contributed to the increased hourly rate of social behaviors exhibited by Laerke. Laerke also differed significantly from Astra in trends between behavior, temperature, and crowd size. Laerke demonstrated increased undesirable behaviors as temperatures increased, similarly to what has been observed in other captive polar bears (Kelly et al., 2015).

Laerke and Jeb: Co-Housing

The introduction and social housing of a polar bear cub to a grizzly bear cub is a rare and unusual endeavor, though a female polar bear cub (Ahpun) and female grizzly bear cub (Oreo) were successfully co-housed at the Alaska Zoo in 2014 (Hardesty, 2002). However, data on such rearing conditions, including at the Alaska Zoo, are not widely available. Providing social and developmental opportunities for orphaned or hand-reared cubs through conspecific or even allospecific housing is well-established (Beecham et al., 2016; Kolter & van Dijk, 2000; Komnenou et al., 2018), but not for cross-species age-mates. Observations of social positive interactions between Laerke and Jeb were highest at their initial introduction, peaking at an average rate of 40 instances per hour in September 2021. Although the average rate of social positive interactions between Jeb and Laerke decreased each month, both their positive and negative social interactions remained substantially higher than Astra's until the month of their separation (March 2022). Some of Jeb's trends in social positive behaviors also demonstrated ties to weather conditions. This may be explained by his use of the pool, which increased in warmer temperatures and conditions. Jeb was largely the initiator of bouts of social play with Laerke, which may be explained by species-specific, sex-specific, or individual-specific trends. Unfortunately, our sample size does not allow us to disentangle these variables.

Tracking trends in both social interactions and social proximity were critical for judging when maximum benefits from Laerke and Jeb's social pairing had been reached. By approximately 16 months old, we had noted a marked decrease in Laerke and Jeb's positive social interactions and their time spent in proximity to each other. Furthermore, their differing biology (both sex- and species-based) meant that Jeb (approximately 158 kg at separation) had outgrown Laerke (approximately 109 kg at separation). This notable size discrepancy likely contributed to care staff increasingly characterizing their interactions as rough. Daily reports from animal care staff entered in the Zoological Information Management System (ZIMS) began reporting roughness from Jeb towards Laerke at the beginning of February with these reports continuing until their eventual separation. Research across multiple species has established sex-based differences in type and intensity of play (Burghardt, 2005; Byers & Walker, 1995; Hill & Ramirez, 2014).

Specifically, males usually exhibit higher degrees of both rough and tumble play and object play than their female counterparts (Burghardt, 2005; Gibson & Mann, 2008; Hassett et al., 2008; Hill & Ramirez, 2014; Meaney et al., 1985). The result of this was a disparity in both body size and intensity of play between the two bears. Their biological differences may have been exacerbated by individual health histories, as Laerke experienced health issues in early life and has always been small, particularly compared to Astra. Ahpun and Oreo were co-housed at the Alaska Zoo for a longer period, but both bears were females and closer in size than Laerke and Jeb. Furthermore, as Astra approached independence, there was a renewed interest in introductions between Astra and Laerke to facilitate their eventual co-housing and transfer to another institution. These factors contributed to the decision to transition Laerke and Jeb away from being co-housed. Following their separation, we did observe instances of undesirable behavior in Jeb, which were not observed during the social housing period. However, these instances were relatively infrequent and of short duration.

Benefits of Play and Ultimate Bear Outcomes

Previous studies have established that play in brown bear cubs can have fitness and multi-year survival benefits (Fagen & Fagen, 2004, 2009). Wild brown bears have been observed engaging in social and solitary play behaviors at three and four years old (Clapham & Kitchin, 2016; Fagen & Fagen, 2004, 2009). Brown bear cubs of multiple age-sex classes are also known to initiate and participate in bouts of play with non-littermates (Clapham & Kitchin, 2016), but it is unclear whether the same phenomenon is observed with maternal polar bear groups. Affording these opportunities to Jeb may have facilitated a more normal social trajectory, while also preparing him for his ultimate transfer to an accredited sanctuary where he maintains a positive social housing situation with other conspecifics. The benefits and success of this unique social pairing may be supported by the eventual social outcomes of Laerke as well, although it is impossible to know how social development for Jeb or Laerke may have unfolded had they never been co-housed. After Astra's separation from Suka, Laerke and Astra were successfully introduced and transferred to another AZA-accredited institution where reports indicate a strong and continued positive relationship between the two bears.

Conclusion

The 2023 Bear TAG Regional Collection Plan provides a strategic plan for the polar bear program which urges institutions to participate in *ex-situ* research that may have impacts on ongoing *in-situ* conservation activities (Vineyard, 2023). Although the neonatal stage is critical for addressing and decreasing first-year mortality, longitudinal developmental studies such as this one inform management strategies for ensuring that surviving cubs thrive into sub-adulthood and enter the AZA population as potential future breeders. These data, while not directly comparable, also offer preliminary insights into behavior of wild yearling and sub-independent cubs, which cannot currently be obtained from the wild population. Finally, we provide a successful report of an alternative social rearing opportunity for a single-housed polar bear cub. While concurrent multi-institutional studies of cub behavior are challenging due to the limitations of the zoo-housed population, future studies even with small sample sizes such as this will provide valuable context, support, or adjustment to the trends reported here.

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References

Andrews, N. L., & Ha, J. C. (2014). The effects of automated scatter feeders on captive grizzly bear activity budgets. *Journal of Applied Animal Welfare Science, 17*(2), 148-156.

Arnould, J. P. Y., & Ramsay, M. A. (1994). Milk production and milk consumption in polar bears during the ice-free period in western Hudson Bay. *Canadian Journal of Zoology, 72*, 1365-1370.

AZA Bear TAG. (2009). *Polar Bear (Ursus maritimus) Care Manual*. Silver Spring, MD: Association of Zoos and Aquariums.

Beecham, J. J., Loeffler, K., & Beausoleil, R. A. (2016). Strategies for captive rearing and reintroduction of orphaned bears. *Journal of Wildlife Rehabilitation, 36*(1), 7-16.

Bekoff, M. (1972). The development of social interaction, play, and metacommunication in mammals: An ethological perspective. *The Quarterly Review of Biology, 47*(4), 412-434.

Berghammer, E. L. (2008). *Effects of enclosure design on the behavior and physiology of the captive grizzly bear (Ursus arctos horribilis* [Master's Thesis, Oklahoma State University]. ProQuest Dissertations and Theses database https://www.proquest.com/openview/7848317cb22751e1a28d424fae90c5c3/1?pq-origsite=gscholar&cbl=18750

Bissonnette, P. (2020). *Adult polar bear behaviour: Using non-invasive techniques to assess social play* [Master's Thesis, University of Manitoba]. http://hdl.handle.net/1993/34986

Bovee, E., Madry, T., Gartland, K. N., & Fuller, G. (2025). Contextual factors associated with fecal glucocorticoid metabolites in juvenile polar bears (Ursus maritimus) and a cohabitating juvenile grizzly bear (Ursus arctos horribilis) at the Detroit Zoo. *Journal of Zoological and Botanical Gardens, 6*(1), 1.

Burghardt, G. M. (2005). *The Genesis of Animal Play: Testing the Limits*. MIT press.

Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *The American Naturalist, 146*(1), 25-40.

Che-Castaldo, J., & Meyerson, R. (2019). *Polar Bear Population Viability Analysis Report*. Population Management Center.

Clapham, M., & Kitchin, J. (2016). Social play in wild brown bears of varying age-sex class. *Acta Ethologica, 19*(3), 181-188.

Cless, I. T., & Lukas, K. E. (2017). Variables affecting the manifestation of and intensity of pacing behavior: A preliminary case study in zoo-housed polar bears. *Zoo Biology, 36*(5), 307-315.

Curry, E., Safayi, S., Meyerson, R., & Roth, T. L. (2015). Reproductive trends of captive polar bears in North American zoos: a historical analysis. *Journal of Zoo and Aquarium Research, 3*(3), 99-106.

Demaster, D. P., & Stirling, I. (1983). The Estimation of Survival and Litter Size of Polar Bear Cubs. *Bears: Their Biology and Management, 5* 260-263.

Derocher, A. E., Andriashek, D., & Arnould, J. P. Y. (1993). Aspects of milk composition and lactation in polar bears. *Canadian Journal of Zoology, 71*, 561-567.

Derocher, A. E., & Stirling, I. (1995). Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. *Canadian Journal of Zoology, 73*(9), 1657-1665.

Deun, G. (1961). Birth of a polar bear cub at Auckland Zoo. *International Zoo Yearbook, 2*(1), 85.

Erwin, J., & Deni, R. (1979). Strangers in a strange land: abnormal behavior or abnormal environments? In E. J., T. L. Maple, & G. Mitchell (Eds.), *Captivity and behavior* (pp. 1-28). New York: Van Nostrand Reinhold Company.

Fagen, R., & Fagen, J. (2004). Juvenile survival and benefits of play behaviour in brown bears, Ursus arctos. *Evolutionary Ecology Research, 6*, 89-102.

Fagen, R., & Fagen, J. (2009). Play behaviour and multi-year juvenile survival in free-ranging brown bears, Ursus arctos. *Evolutionary Ecology Research, 11*, 1-15.

Fernandez, E. J., Yoakum, E., & Andrews, N. (2020). Seasonal and daily activity of two zoo-housed grizzly bears (Ursus arctos horribilis). *Journal of Zoological and Botanical Gardens, 1*(1), 1-12.

Fuller, G., Hamilton, J., & Allard, S. (2021). DNA damage as a potential non-Invasive indicator of welfare: A preliminary study in zoo-housed grizzly bears (Ursus arctos horribilis). *Journal of Zoological and Botanical Gardens, 2*(3), 316-334.

Furnell, D. J., & Schweinsburg, R. E. (1984). Population dynamics of central Canadian Arctic Island polar bears. *The Journal of Wildlife Management, 48*(3), 722-728.

Gartland, K. N., Humbyrd, M. K., Brightrall, T., Meister, B., & Fuller, G. (2024). Behavior of polar bear (Ursus maritimus) cubs post-den emergence at the Detroit Zoo. *Zoo Biology, 43(2),* 149-163.

Gartland, K. N., Humbyrd, M. K., Meister, B., & Fuller, G. (2023). Behavioral development of a captive polar bear (Ursus maritimus) cub in the maternal den. *Zoo Biology, 42*(4), 582-587.

Gibson, Q. A., & Mann, J. (2008). Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Animal Behaviour, 76*(2), 375-387.

Gittleman, J. L., & Oftedal, O. T. (1987). *Comparative growth and lactation energetics in carnivores.* Paper presented at the Symposia of the Zoological Society of London.

Greenwald, K. R., & Dabek, L. (2003). Behavioral development of a polar bear cub (Ursus maritimus) in captivity. *Zoo Biology, 22*(5), 507-514.

Hansson, R., & Thomassen, J. (1983). Behavior of Polar Bears with Cubs in the Denning Area. *Bears: Their Biology and Management, 5*, 246-254.

Hardesty, T. (2002). Playtime with Ahpun and Oreo [DVD]. In. United States: Alaska Video Postcards, Inc.

Harlow, H. F., & Harlow, M. K. (1962). Social deprivation in monkeys. *Scientific American, 207*(5), 136-150.

Hassett, J. M., Siebert, E. R., & Wallen, K. (2008). Sex differences in rhesus monkey toy preferences parallel those of children. *Hormones and Behavior, 54*(3), 359-364.

Hess, J. K. (1971). Hand-rearing Polar bear cubs at St Paul Zoo. *International Zoo Yearbook, 11*(1), 102-107.

Hill, H., & Ramirez, D. (2014). Adults play but not like their young: The frequency and types of play by belugas (Delphinapterus leucas) in human care. *Animal Behavior and Cognition, 1*(2), 166-185.

Jonkel, C. J., Husby, P., Russell, R., & Beecham, J. (1980). The reintroduction of orphaned grizzly bear cubs into the wild. *Bears: Their Biology and Management, 4*, 369-372.

Jonkel, C. J., Kolenosky, G., B., Robertson, R. J., & Russell, R. H. (1972). Further notes on polar bear denning habits. *Bears: Their Biology and Management, 2*, 142-158.

Jungheim, A., Sabo, D., & Bladow, R. (2022). Polar Bear Population Analysis & Breeding and Transfer Plan Polar Bear (*Ursus maritimus*). Population Management Center.

Kelly, K. R., Harrison, M. L., Size, D. D., & MacDonald, S. E. (2015). Individual effects of seasonal changes, visitor density, and concurrent bear behavior on stereotypical behaviors in captive polar bears (Ursus maritimus). *Journal of Applied Animal Welfare Science, 18*(1), 17-31.

Kenny, D. E., & Bickel, C. (2005). Growth and development of polar bear Ursus maritimus cubs at Denver Zoological Gardens. *International Zoo Yearbook, 39*(1), 205-214.

King, N. E., & Mellen, J. D. (1994). The effects of early experience on adult copulatory behavior in zoo-born chimpanzees (Pan troglodytes). *Zoo Biology, 13*(1), 51-59.

Kistchinski, A. A., & Uspenski, S. M. (1972). Immobilization and tagging of polar bears in maternity dens. *Bears: Their Biology and Management, 2*, 172-180.

Kolter, L., & van Dijk, J. (2000). *Rehabilitation and Release of Bears.* Paper presented at the The Evaluation of Bear Rehabilitation Projects from a Conservationist's Point of View: Creating a Linkage between Different Fields of Interests, Rhenen, The Netherlands https://lciepub.nina.no/pdf/634991394615033943_Bear_rehab_guidelines.pdf

Komnenou, A. T., Karamanlidis, A. A., Kazakos, G. M., Kyriazis, A. P., Avgerinou, M., Papakostas, G., Stefanidis, K., & Beecham, J. J. (2018). First successful hand-rearing and release to the wild of two orphan brown bear cubs in Greece. *Journal of the Hellenic Veterinary Medical Society, 67*(3), 163-170.

Larsen, T. (1985). Polar bear denning and cub production in Svalbard, Norway. *The Journal of Wildlife Management, 49*(2), 320-326.

Latham, N. R., & Mason, G. J. (2008). Maternal deprivation and the development of stereotypic behaviour. *Applied Animal Behaviour Science, 110*, 84-108.

Lentfer, J. W., & Hensel, R. J. (1980). Alaskan Polar Bear Denning. *Bears: Their Biology and Management, 4*, 101-108.

Lickliter, R., & Harshaw, C. (2010). Canalization and malleability reconsidered: The developmental basis of phenotypic stability and variability. In Hood, K.E., Halpern, C. T., Greenberg, G., Lerner, R. M. (Eds.) *Handbook of Developmental Science, Behavior, and Genetics* (pp. 491-525).

Lønø, O. (1970). The polar bear (Ursus maritimus) in the Svalbard area. *Norsk Polarinstitutt Skrifter 149*, 1-115.

Martin, P. (1984). The meaning of weaning. *Animal Behaviour, 32*(4), 1257–1259.

McGowan, R. T., Robbins, C. T., Alldredge, J. R., & Newberry, R. C. (2010). Contrafreeloading in grizzly bears: implications for captive foraging enrichment. *Zoo Biol, 29*(4), 484-502.

Meaney, M. J., Stewart, J., & Beatty, W. W. (1985). Sex differences in social play: The socialization of sex roles. In Rosenblatt, J., Beer, C., Bushnel, M. C., & Slater, P. (Eds.), *Advances in the Study of Behavior* (Vol. 15, pp. 1-58): Elsevier.

Meder, A. (1992). Effects of the environment on the behaviour of lowland gorillas in zoos. *Primate Report, 32*, 167-183.

Michalowski, D. R. (1971). Hand-rearing a Polar bear cub at Rochester Zoo. *International Zoo Yearbook, 11*(1), 107-109.

Mitchell, G., Maple, T. L., & Erwin, J. (1979). Development of social attachment potential in captive rhesus monkeys. In J. Erwin, T. L. Maple, & G. Mitchell (Eds.), *Captivity and Behavior* (pp. 59-111). New York: Van Nostrand Reinhold Company.

Pagano, A. M., Durner, G. M., Amstrup, S. C., Simac, K. S., & York, G. S. (2012). Long-distance swimming by polar bears (Ursus maritimus) of the southern Beaufort Sea during years of extensive open water. *Canadian Journal of Zoology, 90*(5), 663-676.

Plowman, A. B. (2008). BIAZA statistics guidelines: toward a common application of statistical tests for zoo research. *Zoo Biology, 27*(3), 226-233.

Polischuk, S. C., Hobson, K. A., & Ramsay, M. A. (2001). Use of stable-carbon and -nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. *Canadian Journal of Zoology, 79*(3), 499-511.

Pollet, T. V., Stulp, G., Henzi, S. P., & Barrett, L. (2015). Taking the aggravation out of data aggregation: A conceptual guide to dealing with statistical issues related to the pooling of individual-level observational data. *American Journal of Primatology, 77*(7), 727-740.

Powell, D. M. (2010). A framework for introduction and socialization processes for mammals. In Kleiman, D.G., Thompson, K.V., and Baer, C.K. (Eds.), *Wild Mammals in Captivity: Principles and Techniques,* (49-61): University of Chicago Press.

Ramsay, M. A., & Stirling, I. (2009). Reproductive biology and ecology of female polar bears (Ursus maritimus). *Journal of Zoology, 214*(4), 601-633.

Reichard, T., Favata, G., Petiniot, C., Gheres, A., Czekala, N., & Lasley, B. (1990). Reproductive management plan of Toledo Zoo lowland gorillas over the past 25 years. *Zoo Biology, 9*(2), 149-156.

Renner, M. J., & Kelly, A. L. (2006). Behavioral decisions for managing social distance and aggression in captive polar bears (Ursus maritimus). *Journal of Applied Animal Welfare Science, 9*(3), 233-239.

Ross, S. R. (2006). Issues of choice and control in the behaviour of a pair of captive polar bears (Ursus maritimus). *Behavioural Processes, 73*(1), 117-120.

Ryan, S., Thompson, S. D., Roth, A. M., & Gold, K. C. (2002). Effects of hand-rearing on the reproductive success of western lowland gorillas in North America. *Zoo Biology, 21*, 389-401.

Sheldon, J. D., Cordero-Aponte, C., Reibel, V., Blair, C. D., Zhu, X., Gerhold, R, Cushing, A., Ramsay, E.C., Dodd, D., & Dennis, M. (2022). Morbidity and mortality of free-ranging American black bears (Ursus Americanus) undergoing rehabilitation in eastern Tennessee, USA, 1996-2021. *Journal of Wildlife Disease, 58*(3), 575-583.

Shepherdson, D., Lewis, K. D., Carlstead, K., Bauman, J., & Perrin, N. (2013). Individual and environmental factors associated with stereotypic behavior and fecal glucocorticoid metabolite levels in zoo housed polar bears. *Applied Animal Behaviour Science, 147*(3-4), 268-277.

Simpson, E. H. (1951). The interpretation of interaction in contingency tables. *Journal of the Royal Statistical Society: Series B (Methodological), 13*(2), 238-241.

Skovlund, C. R., Kirchner, M. K., Contiero, B., Ellegaard, S., Manteca, X., Stelvig, M., Tallo-Parra, O., &Forkman, B. (2023). Qualitative Behaviour Assessment for zoo-housed polar bears (Ursus maritimus): Intra- and inter-day consistency and association to other indicators of welfare. *Applied Animal Behaviour Science, 263,* 105942.

Skovlund, C. R., Kirchner, M. K., Moos, L. W., Alsted, N., Manteca, X., Tallo-Parra, O., Stelvig, M., & Forkman, B. (2023). A critical review of animal-based welfare indicators for polar bears (Ursus maritimus) in zoos: Identification and evidence of validity. *Animal Welfare, 30*(1), 1-18.

Smith, T. S. (2021). Polar bear reproductive and denning behavior. In R. W. Davis & A. M. Pagano (Eds.), *Ethology and Behavioral Ecology of Sea Otters and Polar Bears* (pp. 269-292). Springer.

Stirling, I. (1990). *Polar Bears*. Ann Arbor, MI: The University of Michigan Press.

Stirling, I. (2011). *Polar Bears: The Natural History of a Threatened Species*. Ontario, CA: Fitzhenry & Whiteside.

Stirling, I., & Latour, P. B. (1978). Comparative hunting abilities of polar bear cubs of different ages. *Canadian Journal of Zoology, 56*(8), 1768-1772.

Van de Walle, J., Leclerc, M., Steyaert, S. M., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2019). Proximity to humans is associated with longer maternal care in brown bears. *Behavioral Ecology and Sociobiology, 73*, 1-11.

van Gessel, C. (2015). Polar bear mother-offspring interactions in maternity dens in captivity. *Zoo Biology, 34*(5), 453-459.

Vineyard, T. (2023). *Bear Taxon Advisory Group Regional Collection Plan*. Retrieved from Cleveland, Ohio

Waddington, C. H. (1942). Canalization of development and the inheritance of acquired characters. *Nature, 150*(3811), 563-565.

Wortman, J. D., & Larue, M. D. (1974). Hand-rearing polar bear cubs: Thalarctos maritimus: at Topeka Zoo. *International Zoo Yearbook, 14*(1), 215-218