A R T I C L E

Protection, energetic assistance, or social perks: How do beluga offspring benefit from allocare?

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Abstract

Allocare, care for offspring from nonparents, can carry important benefits for offspring. We investigated the potential benefits of allocare to offspring by examining contexts associated with allocare among St. Lawrence belugas in Sainte-Marguerite Bay, a high-residency area, and the Saguenay Fjord, a transit area. We hypothesized that calves receive similar benefits from mothers and alloparents, namely, protection and energetic benefits, while juveniles associate with alloparents for social purposes. As such, we expected that calves would associate with mothers and alloparents more frequently when exposed to potential dangers, such as adult males and vessel traffic, and in energetically costly contexts, such as the flood tide and during travel, while juveniles would associate with alloparents more frequently during social behavior. We found no trends between allocare and any variables tested. However, we found that calf maternal care in the fjord decreased significantly during socialization, particularly calf-calf socialization. We also found that juvenile maternal care in the fjord decreased significantly when males were present, possibly because juveniles sought associations with males. These findings emphasize the importance of socialization for beluga offspring of all ages. Both maternal care and allocare persisted across contexts in Sainte-Marguerite Bay, highlighting its possible importance as an offspring-rearing ground.

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1 | INTRODUCTION

In some species, offspring receive care from both parents and other group members known as alloparents (Riedman, 1982). Such nonparental care, or "allocare" is often highly beneficial to offspring. Like parents, alloparents can defend offspring from threats or provide protection in potentially dangerous situations. For example, female sperm whales (*Physeter macrocephalus*) stagger their dives such that vulnerable calves are never left alone at the surface during maternal foraging bouts (Whitehead, 1996). Similarly, blue monkey (*Cercopithecus mitis*) alloparents actively defend infants against aggressive conspecifics and retrieve infants when predators are detected (Förster & Cords, 2005). Similar to parents, alloparents can also provide offspring with energetic benefits through nursing, food-sharing, and by facilitating travel (Ross & MacLarnon, 2000). Primate alloparents often carry infants (Altmann & Samuels, 1992), while cetacean alloparents facilitate offspring movement via formation locomotion (Hill & Campbell, 2014; Simard & Gowans, 2004; Waite, 1998). Alloparents may also offer benefits that parents cannot offer, such as the opportunity to expand an offspring's social network through potentially important social bonds (Fairbanks, 1990; Lancaster, 1971; Stanford, 1992). Early social initiation is likely particularly important for species with long-term social bonds and labile group membership, such as belugas (*Delphinapterus leucas*; Michaud, 2005; O'Corry-Crowe et al., 2020).

Like other cetacean mothers, beluga mothers provide sustenance to their offspring, facilitate offspring locomotion, and shield offspring from danger (Hill, 2009; Krasnova et al., 2006, 2014). Beluga calves typically subsist exclusively on their mother's milk during the first year of life, but may continue to nurse for up to 4 years (Matthews & Ferguson, 2015). As relatively weak, uncoordinated swimmers, beluga calves also rely on their mothers for locomotion by drafting in their mother's slipstream, a behavior known as formation locomotion (Krasnova et al., 2009, 2014). As offspring age, their swimming skills improve and they become more independent, initiating more frequent separations from their mother (Krasnova et al., 2014). Following Adrianov et al. (2018) and Vergara & Mikus (2019), we consider that "calves" include neonates and yearlings, while "juveniles" are older offspring, approximately 2–5 years old. When approaching sexual maturity, male offspring are thought to leave their mothers to form or join male-only groups, while female offspring may continue to associate regularly with their mothers for their entire lives (Krasnova et al., 2006, 2014).

Beluga offspring also rely on care from alloparents. Bel'kovitch and Shekotov (1990/1993) reported observations of "kindergarten" groups among free-ranging belugas, where calves associated with immature individuals while mothers were foraging. Krasnova et al. (2006, 2014) also reported wild beluga calves associating with immature individuals, and occurrences of "aunts" attending to calves. In captive studies, Leung et al. (2010) found that a beluga calf was nursed by his half-sister and an unrelated allomother, while Hill and Campbell (2014) found that almost all beluga offspring studied swam in formation with alloparents and were sometimes nursed by alloparents. Recently, Aubin et al. (2021) found that allocare was common among St. Lawrence belugas, as both calves and older juveniles often swam in formation with multiple adults. Among both captive and wild belugas, most alloparental associations are initiated by offspring rather than alloparents (Aubin et al., 2021; Hill & Campbell, 2014), suggesting that offspring derive some benefit from these associations. Such benefits could include protection from threats, energetic benefits, or social benefits. To determine the benefits that beluga offspring receive from alloparents, and whether these benefits mirror those of maternal care, we examined maternal and alloparental associations at two sites in the St. Lawrence Estuary.
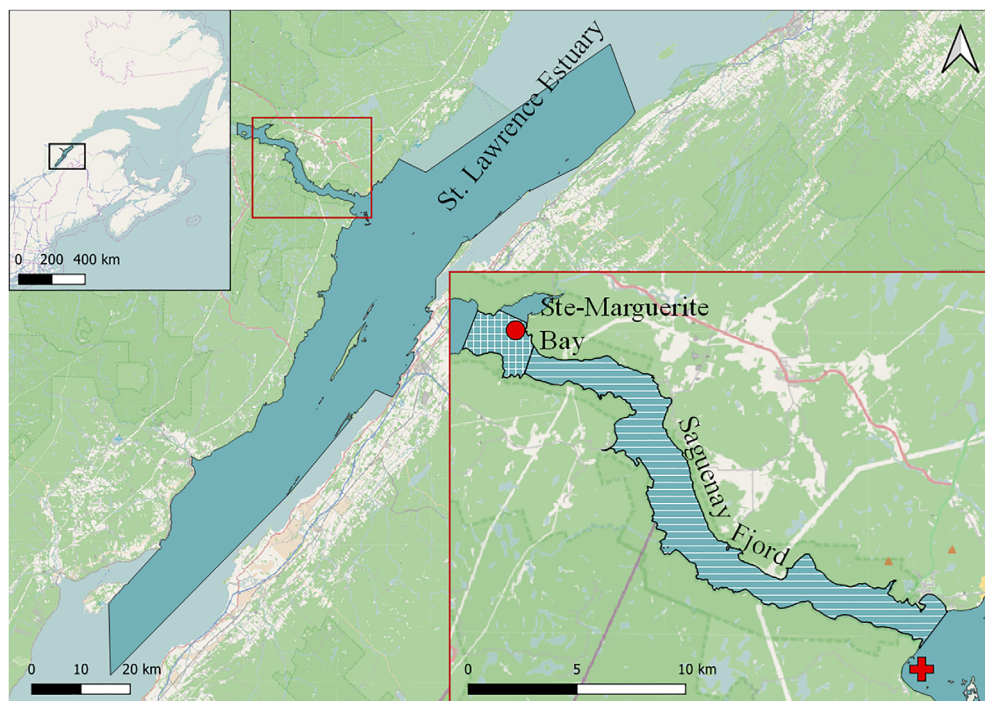
FIGURE 1   Critical habitat of St. Lawrence belugas (DFO, 2012) and extent of the study sites in the Saguenay St. Lawrence Marine Park in Quebec, Canada. In 2016 and early 2017, sampling occurred aboard a research vessel in the Saguenay Fjord (horizontal white hatching). In late 2017 and 2018 sampling occurred from a research platform (indicated by the red circle) in Sainte-Marguerite Bay (white cross-hatching). The red cross shows the approximate location of tidal measurements.

We focused on the Saguenay Fjord, a tributary of the St. Lawrence River, and Sainte-Marguerite Bay, a small bay within the fjord that has been identified as a beluga high-residency area (Figure 1; Lemieux Lefebvre et al., 2012; Ménard et al., 2018). Sainte-Marguerite Bay has long been recognized as an important habitat for St. Lawrence belugas, particularly females with young, and has been hypothesized to function as a feeding ground, rest area, breeding ground, nursery, or social hub (Michaud et al., 1990; Pippard & Malcolm, 1978). Similar patterns of habitat use are observed in Arctic populations, where belugas congregate in shallow bays and estuaries in the summer to molt, rest, feed, care for young, and socialize (Anderson et al., 2017; O'Corry-Crowe et al., 2009; Smith et al., 2017). In contrast, the Saguenay Fjord appears to serve as a transit corridor connecting the St. Lawrence Estuary to Sainte-Marguerite Bay (Ouellet et al., 2021). We obtained a total of 1,846 focal observations of beluga calves and juveniles from the two sites, and identified a series of variables that, if related to maternal care and allocare, may allow us to infer the benefits of allocare to offspring and whether they are similar to the benefits of maternal care.

1.1 | Variables related to possible benefits

1.1.1 | Male presence

Infanticide by males has been reported in many odontocete species (Bowler et al., 2018; Dunn et al., 2002; Towers et al., 2018; Zheng et al., 2016). While infanticide has never been observed among belugas, Loseto et al. (2006) suggested that patterns of sexual segregation among belugas are consistent with a risk of infanticide by males. As

belugas in the St. Lawrence Estuary have no natural predators, adult males may pose the greatest natural threat to young belugas. If mothers and alloparents protect offspring against males, then both maternal care and allocare should occur more frequently when groups of adult males are nearby.

1.1.2 | Vessel traffic

The Saguenay Fjord is an extremely busy waterway, receiving large volumes of vessel traffic from ferries, shipping vessels, and pleasure boats (Ménard et al., 2014). The deleterious effects of vessel traffic and noise pollution on odontocetes are well documented (Gomez et al., 2016; Weilgart, 2007). Specifically, group cohesion and mother-offspring communication may be negatively impacted in noisy environments (Tennessen & Parks, 2016; Van Parijs & Corkeron, 2016; Vergara et al., 2021). If close associations with mothers and alloparents mitigate the risks of offspring separation during periods of vessel disturbance, then the frequency of both maternal care and allocare should increase with vessel traffic.

1.1.3 | Group behavior

The predominant behavioral states in which allocare occurs could allow us to infer why offspring associate with alloparents. For example, if allocare occurs primarily during behaviors associated with travel, then offspring may associate with alloparent for the energetic benefits of formation locomotion. St. Lawrence belugas can cover large distances over the course of a single day and can reach swim speeds of over 20 km/hr (Lemieux Lefebvre et al., 2012). Without the hydrodynamic advantages of formation locomotion, odontocete calves cannot keep pace with adult group members (Weihs, 2004). Alternately, if allocare occurs primarily during behaviors associated with sociality, allocare may serve a social purpose for offspring. Social behaviors among belugas include close physical contact, rubbing, chasing, and socio-sexual behaviors (O'Corry-Crowe et al., 2009). These behaviors likely play an important role in the formation and maintenance of social bonds (Hill et al., 2015, 2018).

1.1.4 | Tide state

For belugas living in estuarine habitats, tidal fluctuations represent one of the most important sources of environmental variation. Belugas frequently time their movements with the tides, preferring to swim upstream with the flood tide (Ezer, 2008; Frost et al., 1985). For Arctic belugas in the Mackenzie River, this pattern may represent an energetic decision, as upstream movement is facilitated when seaward currents are minimized by the influx of tidal waters (Simard et al., 2014). Similar tidally driven movements have been suggested to occur in the Saguenay Fjord (Busque, 2006). As the journey from the mouth of the fjord to Sainte-Marguerite Bay stretches approximately 25 km and features strong currents (Saucier & Chassé, 2000), the flood tide is likely favorable for upstream travel. If maternal care and allocare both increase during the flood tide, particularly in the fjord and while groups are traveling, this would suggest that both mothers and alloparents facilitate long-distance travel for offspring.

1.2 | Hypotheses and predictions for calves and juveniles

Both very young, vulnerable calves and older, more independent juveniles associate with alloparents (Aubin et al., 2021), suggesting that beluga offspring of different ages may derive different benefits from allocare. We hypothesized that calves associate with mothers and alloparents for similar reasons: safety and energetic assistance.

TABLE 1 Predicting how variables relating to potential protective, energetic, and social benefits of associations with mothers and alloparents impact the occurrence of beluga maternal care and allocare, based on hypothesized divergent benefits for calves and juveniles.

Benefit to offspring	Age class benefitting	Variable	Impact on maternal care	Impact on allocare
Safety & protection	Calf	Male presence	Increase	Same as maternal care
		Vessel traffic	Increase	Same as maternal care
Energetic benefit	Calf	Group behavior	Increase during travel	Same as maternal care
		Tide state	Increase during flood tide, during travel and in the fjord	Same as maternal care
Social benefit	Juvenile	Group behavior	No impact	Increase during social behavior

We therefore predicted that both calf maternal care and allocare would increase in the presence of adult males, in the presence of vessels, during travel, and during the flood tide (Table 1). In contrast, we hypothesized that juveniles mainly gain social benefits from allocare and predicted that juvenile allocare would increase during social behavior, while juvenile maternal care would remain constant across behavioral contexts (Table 1).

2 | METHODS

2.1 | Obtaining footage of offspring

We collected footage of female belugas with offspring in the Saguenay-St. Lawrence Marine Park in Quebec, Canada, using unoccupied aerial vehicles (UAVs; Phantom 4 and Phantom 4 Pro, DJI, Shenzhen, China) in the summers of 2016, 2017, and 2018. We recorded footage of belugas from the mouth of the Saguenay Fjord to Sainte-Marguerite Bay (Figure 1). Data collection for this project occurred in two stages. In 2016 and early 2017, sampling was restricted to the fjord and was carried out aboard an 8 m rigid hulled inflatable vessel. In late 2017 and 2018, data collection was carried out from a fixed platform erected in Sainte-Marguerite Bay, and sampling was restricted to the bay. We obtained 156 videos of approximately 15 min each.

2.2 | Continuous behavioral focal sampling of offspring

For all beluga offspring recorded in UAV videos, we conducted continuous behavioral focal sampling following Altmann (1974), using the event recorder JWatcher 1.0 (Blumstein & Daniel, 2007). We classified focal offspring as calves or juveniles based on relative size and morphology (Figure 2). As our UAV system was not specialized for photo-identification, we were unable to differentiate most individuals. We recorded each new observation of an offspring as a new focal individual. Each focal observation consisted of the entire duration of time that an offspring remained in sight or could be distinguished from other offspring.

2.3 | Identifying maternal care and allocare

We considered that maternal care occurred when offspring swam in formation with at least one adult, and that allocare occurred when offspring swam in formation with multiple adults. Other behaviors, such as allonursing and food sharing,

FIGURE 2 Three St. Lawrence beluga offspring (one calf and two juveniles) swimming in formation with adults. Offspring smaller than approximately half of adult body length were classified as calves. Offspring reaching half of adult body length or longer were classified as juveniles.

might also reflect alloparental behaviors. Indeed, allonursing has been observed among captive belugas (Hill & Campbell, 2014; Leung et al., 2010), and the discovery of a lactating, yet presumably post-reproductive female St. Lawrence beluga (Ellis et al., 2018; McAlpine et al., 1999) suggest that allonursing might occur in the wild. However, such behaviors are difficult to observe from UAV footage. Therefore, we focused exclusively on formation locomotion, which likely represents only one aspect of allocare among St. Lawrence belugas. Following Noren (2008), we determined that formation locomotion occurred when offspring swam in close proximity to an adult's flank, just behind its pectoral flipper (Figure 2), or below the adult's tailstock. During formation locomotion, the offspring is pulled along in the adult's slipstream, such that the pair move in almost perfect synchronicity. It is therefore straightforward to determine which adult is "carrying" each offspring, and to determine when offspring move in or out of an adult's slipstream.

We considered formation locomotion to be indicative of maternal care and allocare due to its energetic costs to adults coupled with energetic benefits to offspring (Noren, 2008; Noren & Edwards, 2011; Waite, 1998). However, while formation locomotion allocare is defined by its energetic benefits, the physical proximity between alloparents and offspring could also facilitate offspring defense or social interaction. If a focal offspring only swam in formation with one adult, or if we were uncertain whether a focal offspring swam with more than one adult due to physical distance or a lack of synchronous movement, we considered that allocare had not occurred. We did not attempt to determine which adult was an offspring's mother, only considering that if multiple adults swam with offspring, then at least one was an alloparent. When an offspring swam in formation with only one adult, this adult was presumed to be the mother. These methods were conservative, and likely underestimated the true frequency of allocare. Because beluga groups remain sexually segregated throughout most of the year (Loseto et al., 2006; Michaud, 2005), most belugas observed associating with offspring were likely female. However, as we did not determine the sex of potential alloparents, we use the term "alloparent," rather than "allomother."

2.4 | Interobserver reliability analysis

To ensure the reliability of the main observer (J.A.A.), we trained two additional observers to reanalyze a subset of videos. These observers respectively analyzed 11 and 17 videos, for a total of 28. For all variables of interest, we compared their observations to J.A.A.'s observations using the intraclass correlation coefficient (Koo & Li, 2016).

2.5 | Quantifying explanatory variables

2.5.1 | Vessel traffic

During field observations, the number of vessels within 2 km of the center of the beluga herd was recorded approximately every 30 min. While 2 km may seem a considerable distance, propeller cavitation noise from an ice breaker has been shown to mask beluga calls over a radius of 22 km, while whale-watching boats can mask the calls of orcas (*Orcinus orca*) from up to 14 km away (Erbe 1997, 2002). We assigned each focal observation the vessel count nearest in time to the start of the video. We did not differentiate between small pleasure boats, sight-seeing boats, and the occasional cargo ship. When the UAV was launched from a research vessel in 2016 and 2017, the research vessel was included in the vessel count.

2.5.2 | Male presence

We devised a method to use qualitative observations to assess the presence of adult male belugas in UAV footage. This method relies on morphological and size differences to differentiate adult males from females, in addition to cues obtained from group composition and social behavior (Glabicky et al., 2010; O'Corry-Crowe et al., 2020; Smith et al., 1994; Vladykov, 1944; see Supporting Information for more details). By assessing four binary measures related to body size, morphology, group composition, and group behavior, we determined the likelihood that males were observed in each video. If all four criteria were met, we considered that males were likely present, if no criteria were met, we considered males to be absent, and if more than one but fewer than four criteria were met, we considered that male presence was uncertain. This resulted in three possible categories of male presence for each video: "yes," "no," and "uncertain."

2.5.3 | Group behavior

Two variables were considered as candidates for defining group behavior: "herd movement pattern," determined during field observations, and "predominant group behavior," determined from UAV footage. During field observations, we assessed herd movement patterns as "milling," "multidirectional," or "directional" approximately every 30 min following the Groupe de Recherche et d'Éducation sur les Mammifères Marins's (GREMM) standard sampling protocol (Lemieux Lefebvre et al., 2018). As a herd is defined as all animals within a radius of 2 km, herd movement patterns broadly describe the behavioral context of many groups, and have been shown to accurately capture variations in individual diving behavior (Lemieux Lefebvre et al., 2018).

We performed analyses of "predominant group behavior" at a later date, using the event-logging software BORIS (v. 7.9.19; Friard & Gamba, 2016). Groups were described as "milling/resting," "traveling," or "socializing" using definitions similar to those used by O'Corry-Crowe et al. (2009) and Baker et al. (2017). Group behavior in UAV footage was analyzed by two observers (J.A.A. and M.A.M.), and a subset of focal observations were analyzed by both observers for an interobserver reliability analysis using Cohen's kappa (McHugh, 2012). We assessed group behavior at 20 s intervals during all focal observations, and then determined the predominant group behavior displayed in each focal observation. For the small number of focal observations not associated with a video timecode ($n = 195$), we assigned the predominant group behavior across the entire video to the focal observation.

As the two behavioral variables were strongly correlated ($\chi^2 = 171.1$, $p < .001$), it was not advisable to use both variables in the same model set. Therefore, we used AIC (Akaike's information criterion) analysis to determine which variable best explained occurrences of allocare in the data set and retained this variable as a measure of group behavior.

2.5.4 | Tide state

Water level measurements were obtained from Sainte-Catherine Bay (denoted by a red cross in Figure 1) every 15 min over the time span of the study (Canadian Hydrographic Service, 2020). We used these measurements to determine the peak high tide and low tide nearest in time to the start of each video. We classified the tide state at the beginning of each video as "ebb tide" or "flood tide."

2.6 | Constructing the model sets

Using an information theoretic approach, we constructed a series of generalized linear mixed effect models (GLMMs) incorporating single variables and combinations of the variables described above (Table 2). We used the function "glmer" (Bates et al., 2015) to construct eight sets of models with binomial error structure. GLMMs were used because they allowed us to control for resampling of focal individuals within the same video by including "video" as a random effect. We also included focal observation duration as an offset in all models to account for longer focal observations being more likely to show evidence of maternal care or allocare. Our response variable described whether maternal care or allocare had occurred (1) or not (0) for each individual focal observation. We constructed a total of eight model sets describing calf and juvenile maternal care and allocare in the fjord and in the bay. We separated our observations by site because each site is believed to represent a unique behavioral context for belugas, such that different patterns of maternal care and allocare may be apparent at the two sites. For the model sets testing the occurrence of allocare, we restricted the data set to observations where maternal care occurred, as our methods did not allow us to observe the occurrence of allocare in the absence of maternal care. We used chi-squared tests and regression models to ensure that none of the explanatory variables of interest were inter-correlated. Vessel counts showed very left-skewed distributions and did not follow the critical logistic regression assumption that the independent variable and log-odds of the dependent variable follow a linear relationship, even following variable transformation. Therefore, we converted this count variable into a categorical variable with five levels: 0, 1, 2, 3, and 4+ vessels. We examined the variance inflation factors for each model to determine whether our variables showed multicollinearity and checked the distribution of the model residuals and the homogeneity of variances using the R package DHARMa (Hartig, 2022). All model sets included a null model, which incorporated only the random effect and offset, and a global model that incorporated the random effect, offset, and all fixed variables (Table 2).

TABLE 2 Fixed and random effects and offset included in the generalized linear mixed-effect models in each model set. All models include video as a random effect and the scaled focal observation duration as an offset. We included a null model, incorporating no fixed effects, and a global model incorporating all fixed effects.

| Model | Fixed effects | | | | Random | Offset |
	Vessels within 2 km	Male presence	Behavior	Tidal phase	Video	Obs. duration
Null					X	X
Global	X	X	X	X	X	X
Vessels + males	X	X			X	X
Vessels	X				X	X
Males		X			X	X
Tide + behavior			X	X	X	X
Behavior			X		X	X
Tide				X	X	X

2.7 | Ranking the models

Using AIC, we ranked all models within each model set to determine which fit the data most parsimoniously (Burnham & Anderson, 2002, 2004). AIC analysis allows a set of models constructed from the same data to be compared to determine which models, and therefore which fixed effects, best explain variation in the response variable. As the inclusion of additional fixed effects generally improves the fit of a model to the detriment of parsimony, AIC incrementally penalizes models for each additional fixed effects included (Burham & Anderson, 2002, 2004).

2.8 | Testing the models

We used a conservative approach, considering that only models with AIC <2 showed evidence of strong explanatory power (Burnham & Anderson, 2002). We used the obtained AIC to calculate the evidence ratio (ER) of models relative to the top ranked model. For the top ranked models in each model set, we examined the proportion of variance explained by the fixed effects of each model by calculating marginal R^2 (mR^2) values, as well as the variance explained by both fixed and random effects by calculating conditional R^2 (cR^2) values. For all top models, we examined the effect sizes for each fixed effect by examining their beta coefficients and associated p-values. For variables that appeared significant, we conducted Tukey post hoc tests to determine which levels of the variable were significantly different from each other. We performed all analyses in R (version 3.4.3; R. Core Team, 2013) with packages "lme4" (Bates et al., 2015), "MuMIn" (Barton, 2018), "rsq" (Zhang, 2021), "emmeans" (Lenth et al., 2022), and "sjstats" (Ludecke, 2019).

3 | RESULTS

The initial interobserver analysis suggested that J.A.A. was reliable in identifying the occurrence of maternal care, allocare, and ages of focal offspring. For the 28 videos that were cross-analyzed, all variables compared showed moderate to excellent agreement between J.A.A. and the two secondary observers (Table 3; Koo & Li, 2016). For more details on the calculation of intraclass correlation coefficients, see Aubin et al. (2021). For the nine videos where both J.A.A. and M.A.M. analyzed predominant group behavior, the two observers showed almost perfect agreement, reaching a Cohen's kappa score of 0.88 (McHugh, 2012).

3.1 | Selection of the "group behavior" variable

We compared two proxies for group behavior, predominant group behavior (obtained from UAV footage) and herd movement pattern (obtained during field observations) to determine which best explained the occurrence of allocare.

TABLE 3 Correlation coefficients with confidence intervals comparing J.A.A.'s observations to the two additional observers across a subset of 28 videos. The lower bound of all intraclass correlation coefficient confidence intervals are greater than 0.5 and are therefore considered acceptable by Koo & Li (2016).

Variable of interest	Intraclass correlation coefficient [95% CI]
Number of calf focal observations	0.93 [0.86, 0.96]
Number of juvenile focal observations	0.81 [0.60, 0.91]
Occurrence of maternal care and allocare	0.87 [0.71, 0.94]

We found that predominant group behavior explained the occurrence of maternal care in the full data set considerably better than herd movement pattern (ΔAIC = 4.68) and explained the occurrence of allocare as well as herd movement pattern (ΔAIC = 0.09). Therefore, we used predominant group behavior as the "behavior" variable in all model sets.

3.2 | Response variables

We obtained a total of 1,846 focal observations, including 662 calf focal observations and 1,184 juvenile focal observations. Maternal care was observed in 1,673 focal observations, and allocare was observed in 253 observations. Therefore, the model sets testing maternal care had a sample size of 1,846 focal observations, while the model sets testing allocare had a sample size of 1,673 observations. 545 focal observations occurred in the Saguenay Fjord and 1,301 occurred in Sainte-Marguerite Bay. On average, calf focal observations lasted 118.4 s and juvenile focal observations lasted 69.7 s. Because calves have weak diving abilities compared to juveniles, they spend more time at the surface and are therefore more readily observed in UAV footage. This likely also partially explains our more frequent observations of calf maternal care and allocare. We found that 92.9% observed calves associated with mothers, and 18.6% associated with alloparents. In comparison, 89.4% of observed juveniles associated with mothers and 11.0% associated with alloparents.

3.3 | Explanatory variables

On average, we recorded 1.27 vessels within 2 km of each focal group, and our vessel counts ranged from 0 to 8. We observed 652 focal follows with no vessels, 623 focal follows with one vessel, and 192, 262, and 117 observations with 2, 3, or 4 or more vessels respectively. We observed 783 focal observations where males were absent, 566 focal observations where males were present and 497 where males might be present. We observed 1,237 focal observations in groups whose predominant behavior was milling/resting, 369 in groups that were traveling, and 240 in groups that were socializing. We observed 841 focal observations during the ebb tide and 1,005 focal observations during the flood tide.

3.4 | Model selection

3.4.1 | Calf maternal care

Results from the AIC analysis showed that group behavior significantly impacted the likelihood of calf maternal care in the fjord. For calf focal observations in the fjord, the "Behavior" and "Tide + behavior" models were both ranked as top models, as both were within 2 AIC (Table 4). In both models, the "Socializing" category of the group behavior variable was associated with a negative beta coefficient and a significant p-value ($\beta = -2.60$, $p = .004$ and $\beta = -2.44$, $p = .006$), suggesting that calf maternal care was less likely to occur in groups that were socializing compared to the reference level, "Milling/resting" (Table 5). The fixed effects of the "Behavior" and the "Tide + behavior" models explained 11% and 12% of the variance in the occurrence of maternal care, respectively. The "Tide" variable in the "Tide + behavior" model was not significant, and therefore likely did not contribute much to the explanatory power of the model. Results from the Tukey post hoc test showed that calf maternal care was significantly less likely to occur in groups that were socializing compared to groups that were milling/resting ($p = .01$) or traveling ($p = .001$; Figure 3A). In comparison, calf maternal care in the bay was poorly explained by the variables examined. The Null model, the "Tide" model, and the "Vessels" model were all ranked as top models, suggesting that

TABLE 4 Top ranked models predicting the occurrence of maternal care and allocare for calves and juveniles in the Saguenay Fjord and Ste-Marguerite Bay. Top models and models within 2 AIC of the top model are bolded and considered to be equally likely. AIC weight (AICw) represents the probability that a given model is the most parsimonious, while the evidence ratio (ER) compares the strength of evidence of the top model relative to a given model. Sample sizes are reported for each model set.

	Fjord				Bay			
	Top 5 models	AIC	AICw	ER	Top 5 models	AIC	AICw	ER
Maternal care								
Calf	**Behavior**	**0.00**	**0.55**	**1**	**Behavior**	**0.00**	**0.29**	**1.0**
	Tide + behavior	**1.25**	**0.29**	**1.87**	**Null**	**0.06**	**0.28**	**1.03**
	Global	2.50	0.16	3.49	**Tide**	**0.60**	**0.22**	**1.34**
	Tide	14.27	0.00	1.3e3	**Tide + behavior**	**1.25**	**0.16**	**1.87**
	Null	14.72	0.00	1.6e3	Males	3.93	0.04	7.13
	n = 218				n = 444			
Juveniles	**Males**	**0.00**	**0.76**	**1**	**Null**	**0.00**	**0.35**	**1.00**
	Null	4.52	0.08	9.58	**Tide**	**1.42**	**0.17**	**2.03**
	Behavior	5.31	0.05	14.22	**Vessels**	**1.55**	**0.16**	**2.17**
	Vessels + males	5.89	0.04	19.00	Males	2.35	0.11	3.24
	Tide	6.34	0.03	23.80	Vessels + males	2.67	0.09	3.80
	n = 327				n = 857			
Allocare								
Calf	**Males**	**0.00**	**0.33**	**1.00**	**Null**	**0.0**	**0.45**	**1.00**
	Null	**0.38**	**0.27**	**1.21**	**Tide**	**1.82**	**0.18**	**2.48**
	Behavior	**1.28**	**0.17**	**1.90**	Males	2.29	0.14	**3.14**
	Tide	2.39	0.10	3.30	Vessels	2.92	0.10	4.31
	Tide + behavior	3.28	0.06	5.15	Behavior	3.81	0.07	6.72
	n = 218				n = 414			
Juvenile	**Males**	**0**	**0.45**	**1.00**	**Tide**	**0.00**	**0.45**	**1.00**
	Vessels + males	2.41	0.14	3.34	**Null**	**0.54**	**0.34**	**1.29**
	Global	2.61	0.12	3.69	Tide + Behavior	3.18	0.09	4.90
	Tide + behavior	2.64	0.12	3.74	Behavior	4.00	0.06	7.39
	Tide	3.23	0.09	5.03	Males	4.32	0.05	8.67
	n = 280				n = 778			

the random effect and offset were responsible for most of the variation in maternal care, rather than any of the fixed effects examined (Table 4).

3.4.2 | Juvenile maternal care

We found that juvenile maternal care in the fjord was best explained by the presence of males. The "Males" model was ranked as the only top model for observations of juvenile maternal care in the fjord and was 9.6 times more likely than the Null model, ranked second. Further examination of the top model showed that juvenile maternal care was least likely to occur when males were present ($\beta = -1.70$, $p = .003$; Table 5). Male presence explained 6% of

TABLE 5 Top ranked models predicting calf and juvenile maternal care and allocare in the Saguenay Fjord. Calf maternal care was best explained by group behavior, while juvenile maternal care was best explained by male presence. Variables associated with *p*-values < .05 are bolded. Juvenile allocare was poorly explained by male presence, despite the "Males" model ranking highly during AIC analysis. Marginal R-squared (mR^2) reflects the variance explained by the fixed effects alone, while conditional R-squared (cR^2) reflects the variance explained by the entire model. "Behavior: milling/resting," "Tide: ebb," and "Males present: yes" were always used as the reference categories for other levels of the Behavior, Tide, and Male Presence variables.

Age class	Top model	mR^2	cR^2	Fixed effects	β	p
Maternal care						
Calf	Behavior	0.11	0.28	**Behavior: socializing**	**−2.89**	**.004**
				Behavior: traveling	2.18	.06
	Tide + behavior	0.12	0.27	Tide: flood	0.66	.47
				Behavior: socializing	**−2.44**	**.006**
				Behavior: traveling	2.11	.07
Juvenile	Males	0.06	0.11	Males present: uncertain	−0.25	.63
				Males present: yes	**−1.70**	**.003**
Allocare						
Juvenile	Males	0.004	0.02	Males present: uncertain	−1.817	.07
				Males present: yes	−0.009	.99

the variance in juvenile maternal care. Results from the Tukey post-hoc test showed that juvenile maternal was significantly less likely to occur when males were present, compared to when males were absent (*p* = .007), and somewhat less likely to occur when male presence was uncertain, though not significantly so (*p* = .08; Figure 3B). Similar to calf maternal care, juvenile maternal care in the bay was poorly explained by the examined variables, as the null model was ranked as a top model (Table 4).

3.4.3 | Calf allocare

Results from the AIC analysis suggest that the occurrence of calf allocare at both sites was poorly explained by the variables examined. For observations in the fjord, the "Males," "Null," and "Behavior" models were all ranked as top models, suggesting that the random effect and offset best explained the occurrence of allocare (Table 4). Similarly, for calf observations in the bay, the "Behavior," "Null," and "Tide" models were all ranked as top models, suggesting that the fixed effects examined had little impact on the occurrence of allocare.

3.4.4 | Juvenile allocare

Juvenile allocare in the fjord was also poorly explained by the variables examined. The "Males" model was ranked as a top model (Table 4), but only explained 0.4% of the variance in juvenile allocare occurrence (Table 5). The "Uncertain" level of the male presence variable was almost significantly different from "Yes," the reference level (*p* = .07; Table 5) but a Tukey post hoc test showed no significant differences between the two categories (*p* = .16), nor between any other pairings. A similar lack of trends was observed for juvenile allocare in Sainte-Marguerite Bay, as the "Tide" and "Null" models were both top-ranked (Table 4).
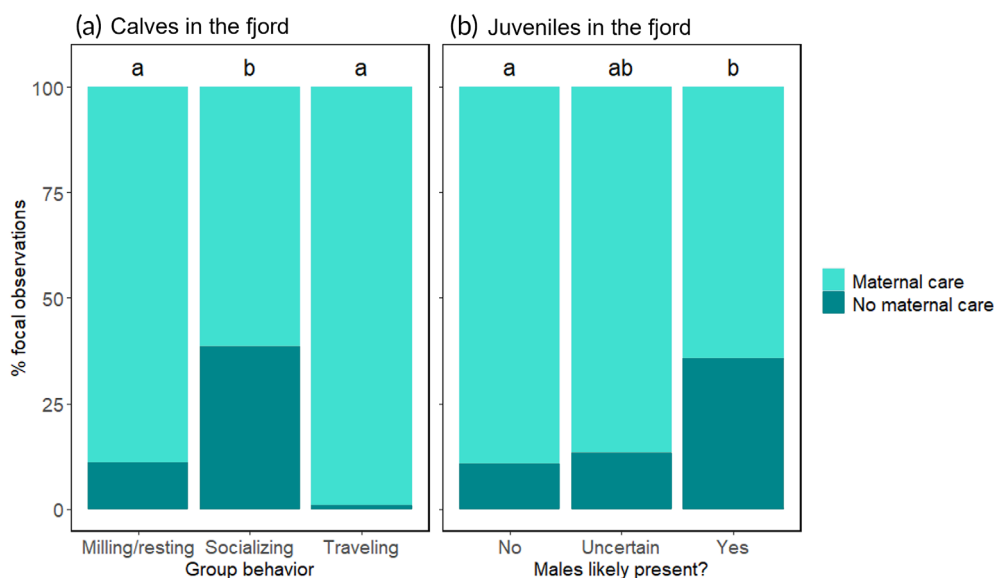
FIGURE 3 A: Percentage of calf focal observations in the fjord that showed evidence of maternal care for groups that were milling/resting ($n = 100$), socializing ($n = 13$), and traveling ($n = 105$). Maternal care was significantly less likely to occur in groups that were socializing compared to groups that were milling/resting ($p = .01$) or groups that were traveling ($p = .001$). B: Percentage of juvenile focal observations in the fjord that showed evidence of maternal care when males were absent ($n = 225$), when male presence was uncertain ($n = 60$), and when males were likely present ($n = 42$). Maternal care was significantly less likely when males were present compared to when males were absent ($p = .007$).

4 | DISCUSSION

We hypothesized that St. Lawrence beluga calves and juveniles receive different benefits from allocare: protective and energetic benefits for calves, and social benefits for juveniles, and that calves would receive similar benefits from maternal care and allocare. We predicted that both calf allocare and maternal care would increase in the presence of males, as vessel traffic increased, and in traveling groups, particularly during the flood tide and in the fjord. However, we instead found that calf maternal care in the fjord decreased during social behavior, and that calf allocare did not vary as a function of any of the variables examined. We also predicted that juvenile allocare would increase in groups engaged in social behavior. Instead, we found that juvenile maternal care in the fjord decreased when males were present and found no trends in juvenile allocare. As such, we found no support for our hypothesis that calves benefit from both maternal care and allocare through enhanced protection and energetic benefits, while juveniles associate with alloparents for social purposes.

4.1 | Traveling behavior

We found that calf maternal care and allocare was no more likely to occur when groups were traveling, despite the apparent energetic benefits of doing so. We do not suggest that the energetic benefits of maternal care during travel are unimportant to offspring; the importance of maternal formation locomotion among cetaceans is well established (Noren, 2008; Noren et al., 2008; Weihs, 2004). Instead, it seems likely that maternal care is so prevalent across behavioral contexts that we cannot tease apart its benefits by examining the behavioral contexts in which it occurs.

Indeed, we observed only one instance of a calf that did not receive maternal care during traveling behavior, yet our analyses showed that maternal care was no more likely to occur during travel than during milling/resting.

As allocare was much more rarely observed, it seems likely that there would be a clear increase in allocare during travel if offspring associate with alloparents for energetic benefits. However, we observed no such trend at either site. This may suggest that the energetic benefits of allocare are not particularly important to offspring, possibly because these needs are met primarily by their mothers. It may also suggest that other benefits of allocare, such as protective and social benefits, are equally important to calves.

4.2 | Social behavior

We found that calf maternal care in the fjord decreased during social behavior. Upon reexamining the few instances of social behavior reported in the fjord, we found that four of these 13 focal observations reflected apparent play behavior between calves, and each of these four observations occurred without maternal care. Indeed, when mothers dove, they sometimes left their calves alone at the surface. During these separations, calves often engaged in chasing behavior, which may reflect play. Such playful interactions between calves have been reported among both captive and wild belugas (Hill, 2009; Krasnova et al., 2014). Krasnova et al. (2014) describe these interactions as "tagging" and suggest that such locomotive play may serve to improve coordination and develop hierarchical relationships. Therefore, separations from their mothers may afford important opportunities for calves to develop important motor and social skills.

Unexpectedly, we found that juvenile allocare was no more common in groups engaged in social behavior. During social behavior, belugas spend much of their time in close physical contact, rubbing against each other, orienting towards each other, and engaging in socio-sexual behaviors (O'Corry-Crowe et al., 2009). Such behaviors are likely important for the formation and maintenance of social bonds among belugas (Hill et al., 2015, 2018). However, as we did not observe an increase in juvenile allocare in groups that were socializing, it seems likely that the potential social benefits of allocare are not the main benefit driving juveniles to associate with alloparents, or that the social benefits of allocare are not associated with formation locomotion, our measure of allocare. Offspring may have associated with alloparents during social behavior, but we would not have labeled these interactions as allocare if offspring were not in formation with adults. Alternately, it is possible that the social opportunities of allocare primarily occur outside of the group-wide surface social behaviors that are most apparent in UAV footage.

4.3 | Male presence

We predicted that calf maternal care would increase in the presence of adult males, but this prediction was not met at either site. Once again, it seems likely that maternal care was so prevalent across contexts as to obscure any increase in maternal associations in potentially high-risk contexts. We also expected that allocare would increase in high-risk contexts because alloparents can provide additional protection to offspring, as has been observed in blue monkeys (Förster & Cords, 2005). The opposite prediction is also plausible: in high-risk contexts, offspring may prefer to remain near their mothers, foregoing alloparental associations. However, neither trend was observed.

Unexpectedly, we found that juvenile maternal care in the fjord was less likely to occur in the presence of adult males. It is possible that, when adult males are nearby, juveniles are more likely to separate from their mothers with the goal of associating with males. In captive settings, adult male belugas frequently associate with juvenile males, and these associations are likely important for the socio-sexual development of male belugas (Hill et al., 2015; Mazikowski et al., 2018). Association with males could have been mistaken for maternal and alloparental associations, thereby inflating the rate of maternal care and allocare, but this was not observed. Two scenarios might explain the observed trend: (1) juveniles left their mothers to associate with males but did not engage in formation

locomotion with males or (2) juveniles left their mothers to associate with males, but we did not observe these associations as we preferentially followed females with offspring. Alternately, it is possible that juveniles were more likely to swim alone when males were present because their mothers were associating with males. However, this seems unlikely, as most conceptions in the St. Lawrence occur from April to June (Vladykov, 1944), while our study period ran from late June to late August.

Although we assumed that adult males generally pose a risk to beluga offspring, our observations of male behaviors toward offspring suggest a mix of agonistic and affiliative associations. During one notable observation, a very large individual that appeared to be male rapidly approached two presumed females with small calves. Both females quickly swam away, taking turns swimming in formation with both calves at once. Given this evasive response, it seems likely that the male was perceived as a threat. We also observed one instance where a presumed male repeatedly bit and thrust its genitals against a juvenile. However, we also observed individuals that appeared to be male swimming in formation with offspring. These individuals were classified as alloparents and showed no agonistic behaviors towards the offspring. In one instance, a group of presumed males swam in formation with a lone calf. While our observations are anecdotal, they suggest a more nuanced interpretation of adult male behavior: rather than representing a constant threat to offspring, adult males may often behave neutrally towards offspring, and even be sought out as alloparents.

4.4 | Vessel traffic

While our findings suggest no link between offspring care and vessel traffic, they certainly show a high potential for disturbance. In Sainte-Marguerite Bay, almost half of all focal observations occurred with at least one vessel within 2 km of the belugas, and one third of focal observations in the Saguenay Fjord occurred with at least one other vessel in addition to the research vessel. This high degree of cooccurrence is concerning, as anthropogenic disturbance has been identified as a major threat to this endangered population (Department of Fisheries and Oceans, 2014). Indeed, St. Lawrence belugas show several behavioral responses to vessel disturbance (Blane & Jaakson 1994; Lesage et al., 1999; Scheifele et al., 2005), and vessel traffic is known to reduce foraging, social cohesion, and communication range in belugas and other odontocetes (Aguilar Soto et al., 2006; Finley & Davis, 1984; Van Parijs & Corkeron, 2016; Vergara et al., 2021). However, the type of vessel disturbance encountered is likely to impact the severity of the response. Although we grouped all vessel types together, this is likely not how belugas experience vessel traffic. Indeed, Lesage et al. (1999) found that St. Lawrence belugas showed more persistent reactions to a large ferry than to a small motorboat. Therefore, it is possible that finer measures of vessel traffic are needed to understand how vessel traffic impacts allocare.

4.5 | Tide state

We saw no pattern suggesting that beluga calves primarily associate with mothers and alloparents during the flood tide for assistance during long-distance upstream travel in the Saguenay Fjord. Indeed, we found no correlation between either maternal care or allocare and tide state, for either age class, at either site. It is possible that other behavioral impacts of the tides obscured the possible link between the flood tide and upstream travel. While we emphasized the importance of tides in dictating movement patterns, tides also impact the distribution of prey species (Simard et al., 2002) and beluga feeding behaviors (Ezer et al., 2008; Huntington, 2000). Therefore, if beluga offspring associate with alloparents while their mothers are foraging, as has been observed among sperm whales (Whitehead, 1996) we might expect to see a correlation between allocare and tide state, but only in prey-rich areas. More research is needed to understand how tidal fluctuations in the St. Lawrence Estuary impact the behavior of belugas.

4.6 | Differences between the Saguenay Fjord and Sainte-Marguerite Bay

It may be noteworthy that the only significant trends observed occurred in the fjord, while in the bay none of the variables observed impacted maternal care. Maternal care was almost omnipresent at both sites, but we nonetheless noted a slight increase in maternal care in the bay: 91.6% of offspring in the bay associated with mothers, compared to 88.3% for offspring in the fjord. A similar trend was observed for allocare: 14.8% of offspring in the bay associated with alloparents, compared to only while 11.2% for offspring in the fjord. These findings are consistent with the hypothesis that Sainte-Marguerite Bay is a particular important site for females with offspring and may function as a nursery or rearing ground (Lemieux Lefebvre et al., 2012; Ménard et al., 2018; Michaud et al., 1990; Pippard & Malcolm, 1978). Similar to Ouellet et al. (2021), we also found support for the idea that the Saguenay Fjord primarily represents a transit corridor between Sainte-Marguerite Bay and the St. Lawrence Estuary. We found that traveling was the predominant behavior in the fjord: 53.6% of focal observations in the fjord occurred in groups that were traveling, compared to only 5.9% in the bay. However, comparisons between the two sites should be interpreted with caution, as the data collection methods at the two sites varied considerably (most notably, the use of a research vessel in the fjord), and this may limit our ability to compare the results obtained at the two sites.

4.7 | Limitations

This study was constrained by certain limitations. We assumed that offspring that associated with a single adult were associating with their mother, but each adult observed could theoretically be an alloparent. Therefore, we likely underestimated the true prevalence of alloparental associations. The way in which alloparents were defined also means that maternal care and allocare were not truly independent, as observations of allocare required that maternal care was also observed. This means that it was not possible to identify a situation in which maternal care decreased while allocare increased. We were also limited in the types of behaviors observed. Using aerial footage, it was only possible to assess surface and near-surface behaviors, but patterns of allocare underwater may differ significantly from those observed at or near the surface. Our observations also tended to be short, as the belugas dove frequently, and it was often impossible to reidentify focal offspring based on unique coloration or morphology. Because we focused on formation locomotion, the most easily observed form of offspring care among belugas, we likely did not capture the full range of alloparental behaviors exhibited by belugas. Other forms of allocare, such as allonursing, might follow different patterns than those observed here. It is notable that we defined formation locomotion by its energetic costs to adults and energetic benefits to offspring. Therefore, the mere fact that both maternal care and allocare were observed in most contexts suggests that energetic benefits likely carry some importance for both calves and juveniles.

4.8 | Conclusion

Our hypothesis that allocare, like maternal care, offers energetic and protective benefits to calves, while juveniles associate with alloparents for social purposes was not supported. While it seems likely that allocare provides both calves and juveniles with a rich suite of benefits, we were unable to conclusively define such benefits. We did, however, find that calf maternal care in the Saguenay fjord was least likely to occur in groups that were socializing, likely because calves separate from their mothers to socialize with other calves. We also found that juvenile maternal care in the fjord was least likely to occur in the presence of males, possibly because juveniles separate from their mothers to investigate and associate with male groups. It is noteworthy that the only two variables that reduced the frequency of maternal care both appear to reflect the social needs of offspring. Calves may forego maternal care to associate with other calves, while juveniles may forego maternal care to associate with adult males. Given the

importance of maternal care for offspring survival, it seems apparent that socialization is crucially important to beluga offspring of all ages. Our findings also show that allocare occurs across a range of behavioral and environmental contexts. While we were unable to pinpoint the exact benefits of allocare, its persistence across different contexts suggests that allocare is an essential component of the daily lives of beluga offspring. As our understanding of the social lives of belugas and other odontocetes grows more complex, it may be fitting that patterns of allocare defy simplistic categorization.

AUTHOR CONTRIBUTIONS

Jaclyn A. Aubin: Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review & editing. **Robert Michaud:** Funding acquisition; project administration; resources; validation; writing – review and editing. **Eric Vander Wal:** Funding acquisition; project administration; supervision; validation; writing – review and editing.

ETHICAL NOTE

Our fieldwork methods were reviewed and approved by the Memorial University Animal Care Committee (Animal Use Protocol: 20190640). Our research and specifically the use of research UAVs in the Saguenay-St. Lawrence Marine Park was covered by research permit SAGMP-2018-28703 issued by Parks Canada and QUE-LEP-001-2018 issued by Fisheries and Oceans Canada. At all times, we maintained the UAV at an altitude greater than 20 m, as low altitude UAV flights may disturb marine mammals (Smith et al., 2016). We noticed few apparent reactions to the UAV.

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